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ROLE OF DISPERSAL AND MORTALITY IN THE DIFFERENTIAL SURVIVAL OF MALE AND FEMALE RICHARDSON'S GROUND SQUIRRELS

by

© SHEILA M. SCHMUTZ

A THESIS

SUBMITTED TO THE FACULTY OF GRADUATE STUDIES AND RESEARCH

IN PARTIAL FULFILLMENT OF THE REQUIREMENTS FOR THE DEGREE

OF MASTER OF SCIENCE

DEPARTMENT OF ZOOLOGY

EDMONTON, ALBERTA

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THE UNIVERSITY OF ALBERTA

FACULTY OF GRADUATE STUDIES AND RESEARCH

The undersigned certify that they have read, and recommend to the Faculty of Graduate Studies and Research, for acceptance, a thesis entitled "Role of dispersal and mortality in the differential survival of male and female Richardson's ground squirrels" submitted by Sheila M. Schmutz in partial fulfilment of the requirements for the degree of Master of Science.

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Supervisor

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Date.....April 21/77.....

post-emergence. Furthermore, annual loss was significantly greater among juvenile males that immigrated than among those born and remaining on the study area.

The third hypothesis suggests that predation may be directed disproportionately towards males. Evidence from this study showed that avian predation took more juvenile males than juvenile females. The sex ratio of adult squirrels killed by raptors did not vary significantly from that in the live population.

The last hypothesis suggests that overwinter mortality may kill more males than females because of differences in length of hibernation periods or suitability of hibernacula. Evidence from this study does not support this hypothesis as estimates of overwinter loss, although high, were not different between the sexes. Theoretical implications of an unbalanced sex ratio are discussed. Practical implications for ground squirrel control based on removal studies are also discussed.

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Introduction

Richardson's ground squirrel (Spermophilus richardsonii) is a common mammal on the prairies where it has been referred to erroneously as a "gopher" since at least 1875 (Coues, 1875). This squirrel is distributed "from the plains of Alberta, Saskatchewan and Manitoba...south into Montana, North Dakota, northeastern South Dakota, Eastern Idaho, Wyoming and northern Colorado" (MacClintock, 1970:37). Adults are about 311 mm long (Bailey, 1893) and vary in weight from 300 g to 500 g depending on time of year (Bailey, 1926).

They are gregarious, many animals occurring in a small tract of land with few between these concentrations (Coues, 1875). They live in burrows (Coues, 1875) that are usually located on ridges (Howell, 1938) and in which they hibernate during much of the year (Gunderson, 1961). They emerge from hibernation in late March or early April (Bailey, 1926), males about 1-2 weeks prior to females (Clark, 1970; Yeaton, 1972) and breed soon after (Bailey, 1926). Both yearlings and older adults are sexually mature (Michener and Michener, 1973). Polygamous mating occurs (Coues, 1875). The gestation period is about 28 days and only one litter is produced per year (Howell, 1938). The young spend 3 to 4 weeks below ground in the natal burrow before emerging for the first time (Wehrell, 1973) in late May or early June (Yeaton, 1969). Adult males begin entering hibernation in early July (D. Michener, 1974) and adult females follow in

mid-July (Yeaton, 1969). The young or juveniles enter hibernation in September (Yeaton, 1969), females preceding males (D. Michener, 1974).

An unbalanced sex ratio appears to be characteristic of breeding populations of Richardson's ground squirrels (Nellis, 1969; Michener and Michener, 1971; Sheppard, 1972; Wehrell, 1973; Dorrance, 1974; Goulet and Sadleir, 1974). At birth sex ratios do not differ significantly from 1:1 (Gunderson, 1961; Nellis, 1969; Michener and Michener, 1971; Sheppard, 1972; Michener and Michener, 1977) but among adults, females usually outnumber males by approximately 3:1 (Sheppard, 1972; Goulet and Sadleir, 1974; Michener and Michener, 1977).

The causes of this change in the sex ratio have been the subject of speculation. Several hypotheses have been suggested to explain it. One hypothesis proposes that loss occurs during early spring. Dorrance (1974) suggested that cold weather, snow cover, and shortage or inaccessibility of food may increase the mortality of adult males at this time and that these factors affect adult females to a lesser degree since they emerge later. He suggests that snow cover may make it difficult for squirrels to relocate their burrow openings. If the hypothesis is correct the loss of adult males should be greater than of adult females during the first few weeks following emergence from hibernation.

The early spring period also may be a time of greater vulnerability to predation for males than females because it

is the breeding season. If the sex ratio favors adult females by the time that breeding occurs, then each male will need to breed more than one female (Yeaton, 1972; Michener and Michener, 1977). This would necessitate considerable movement by males at this time.

The sex ratio already may be altered in favor of females at the time of emergence from hibernation. A second hypothesis, involving juvenile loss during the summer, may explain this phenomenon. Dorrance (1974) reported greater loss of juvenile males than juvenile females between mid-June and mid-July and greater ingress of males. Several reports in the literature suggest juvenile males move more than juvenile females: Yeaton (1972) reported that young males disperse farther than females based on recapture data; Wehrell (1973:94) stated that "[d]uring the summer wandering occurs among young males,...perhaps resulting in loss of orientation and hence dispersing." Thus, if males disperse either at greater frequencies or over greater distances than females, then the recorded loss of marked males and/or the addition of unmarked males into a local population, should exceed comparable figures for females.

A third hypothesis involves differential predation. If juvenile males disperse at greater frequencies or over greater distances than juvenile females, they may be more vulnerable to predation (D. Michener, 1972). This may result in more males emigrating from a local population than immigrating into it. Since Richardson's ground squirrels

are known to be subject to both avian and mammalian predation (Gunderson, 1961; Quanstrom, 1968; Clark, 1970; D. Michener, 1972; Wehrell, 1973; Dorrance, 1974), it is possible to check the hypothesis by recording the sex ratio among the squirrels killed by such predators. The main prey of ferruginous hawks (Buteo regalis) and Swainson's hawks (Buteo swainsoni) is Richardson's ground squirrels (Bailey, 1926; Banfield, 1974). Since these two hawks nest in proximity to populations of Richardson's ground squirrels it should be possible to compare the sex ratio in the kill with that in the population studied.

Michener and Michener (1977) suggest that overwinter mortality may alter the sex ratio. Since entry into hibernation within any sex-age class may extend over 1 month (Wehrell, 1973; Goulet and Sadleir, 1974; Michener and Michener, 1977), it is difficult to categorize the disappearance of an animal, after the onset of the hibernation period, as either hibernation, emigration or death. Therefore most hypotheses erected to explain differential loss of the sexes are based on survival from one breeding season to the next. These either include loss throughout the year, rather than only overwinter loss, or provide intuitive arguments to suggest why overwinter loss may be differential. Such arguments include availability of hibernation burrows, differing periods spent below ground and varying prehibernation weights. If differential loss is recorded during the non-hibernating period different rates

of loss for the sexes between years can not be attributed entirely to differential rates of overwinter mortality, but, if no differential loss is recorded during the non-hibernating period, then different rates of loss for the sexes between years must be the result of differential overwinter mortality.

This study was undertaken to test these hypotheses using populations of Richardson's ground squirrels in an area of grazed grasslands near Hanna, Alberta. It complements a study of three species of avian predators conducted in this area at the same time.

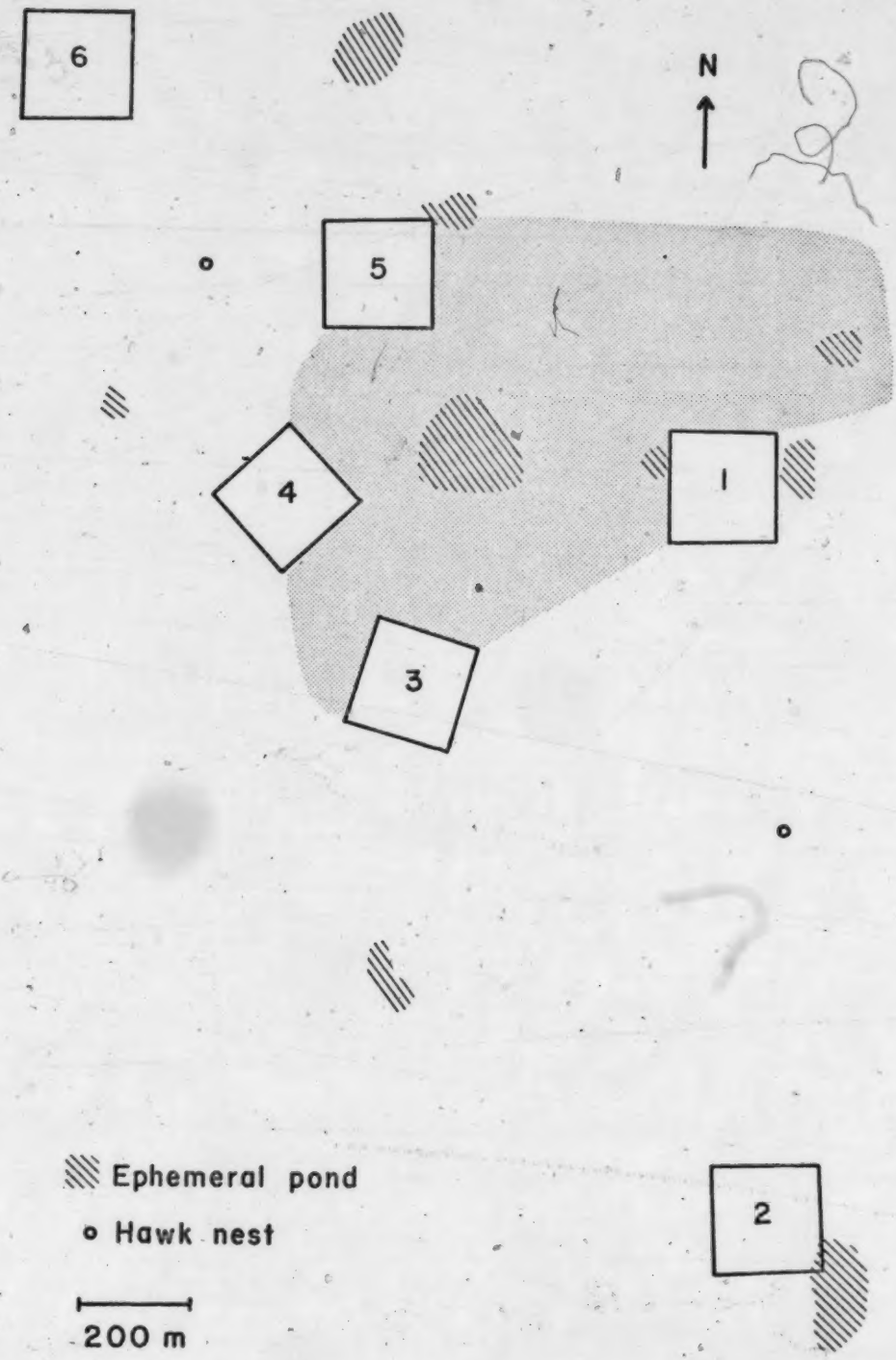
Materials and Methods

The study area (51° 25' N, 111° 48' W) was located 29 km southeast of Hanna, Alberta within the Bullpound Community Pasture. This pasture, farmed in the 1930's but since abandoned, reverted to a semi-natural grassland. The vegetation is dominated by grasses but contains patches of low shrubs throughout. Isolated clumps or rows of trees in the area are the survivors of shelterbelts planted before 1940.

The area is classified as mixed-grass prairie (Webb et al., 1967). The altitude of the study area ranges from 789 to 800 m. "Gently rolling knots and depressions" (Webb et al., 1967) and coulees dot the area. Brown soil is the characteristic type. The climate is continental, the summers are hot but short and the winters are long and cold. The minimum temperature was -36.7°C and the maximum temperature was 35.0°C (recorded at the Brooks weather station) in the 2 years of this study. The average annual precipitation ranges from 28 to 35.5 cm (Webb et al., 1967). The precipitation recorded at Brooks, Alberta was 54.6 cm in 1975 and 33.7 cm in 1976.

Two sets of three 4-ha plots were established in May, 1975 (Fig.1). This was the maximum size of plot which could be trapped completely in 1 week. Towards the center of each group of three plots, at a distance of 0.4 to 1.2 km, was the nest of a ferruginous hawk. The plots were located around nests to determine the frequency at which marked

Figure 1. Study area with six study plots. The shaded portion was trapped in August, 1975.


6
N
5
4
1
3
2
Ephemeral pond
Hawk nest
200 m

squirrels were killed by raptors. Although the ground squirrel population did not appear to be separable into discrete local populations, the density of squirrels varied considerably over the area. Therefore, the plots were located not only within the specified distances from the hawk nests but also in locations where ground squirrels were relatively abundant (Fig. 1). The plots were gridded into 16 squares (50 m x 50 m) by means of a series of stakes. All plots were grazed by cattle during part of both summers of the study.

Squirrels were trapped between April 15 and September 30, 1975 and March 21 and October 20, 1976 whenever weather conditions permitted (no rain and less than gale force winds). Plots within the study area were trapped in rotation. From May through August, two plots were trapped concurrently because two people were available for trapping. From 5 to 8 days were required to capture all animals known to be on each plot. Thereafter trapping was continued an additional 2 days to assure that all squirrels on the plot were indeed caught and marked. As a result, 7 to 10 days were usually spent on each plot before moving to the next. In addition to the plot itself, a buffer zone extending out approximately 50 m around each plot was also trapped, albeit less rigorously. During August, 1975 a third assistant trapped at random in areas between four of the six plots (Fig. 1) to record the locations of marked animals that had left the plots.

I used live traps (Tomahawk Live Trap Company, Tomahawk, Wi; #102 and #103 traps) baited, at least once a day, with a mixture of wheat and peanut butter in 1975 and with peanut butter alone in 1976. Two to four traps were placed at burrow entrances, using the method of D. Michener (1972), and marked by a small plastic flag. They were checked every 0.5 to 1 hour.

Upon initial capture each animal was tagged with two identically numbered metal tags (National Band and Tag Co., Newport, Ky.; Monel size 1), one in each ear. I also clipped one hind toe on each animal to identify the plot on which it was originally captured should only the posterior portion be found in a hawk nest. Sex, age, weight and location were recorded at each capture. Sex was based on the external genitalia. Age was recorded as "juvenile" (born during the present year) or "adult" (born before the present year). "Older adult" will be used subsequently to refer to marked animals known to be at least 22 months of age. "Yearlings" were those animals born and marked in 1975 and recaptured in 1976. Animals trapped in 1976 for the first time but not born during that year were simply classified as adults. Weight was recorded to the nearest 5 g using a 1000 g Pesola spring scale. Location was recorded within 5 m using the staked grid system previously described. Animals were released at their capture site after handling which took a maximum of 5 minutes.

The boundaries of the plots transected home ranges of some individuals. Because the buffer area was trapped also, I was usually able to designate the home burrow of a squirrel as the one at which it was most often trapped. Squirrels were considered residents of the plots if their home burrow or at least 50% of their capture sites were within the plot boundaries. Data from all resident animals was used in the calculations.

In order to establish the length of the breeding season, the left testis was removed from males killed in the area, preserved in Bouin's solution, and weighed to the nearest 0.0001 g. Weights were recorded from an analytical balance when I returned to the laboratory in the autumn. To determine whether differential loss was occurring between the sexes in spring, males and females were trapped from first emergence. Rates of loss of marked animals were compared between the sexes for this period. Greater mortality or dispersal caused by weather or breeding should be reflected in a greater loss of males during the first month after emergence. Although dispersal may often be reflected in increased loss or gain of individuals, increased movement of individuals that remain in the population also may reflect a greater tendency to disperse among a particular sex and age class. Movement was calculated as the shortest distance between two consecutive capture points.

Juvenile dispersal during the summer may alter the sex ratio. To establish the extent of immigration or emigration, juvenile squirrels were trapped at first emergence and thereafter at monthly intervals. Loss of individuals and number unmarked, presumably ingressing individuals, were compared between the sexes. It may be difficult to be certain that unmarked squirrels are immigrants in all cases. To alleviate this uncertainty, all adult squirrels were removed from two study plots in 1976, thus, all squirrels trapped thereafter were immigrants. If males disperse more than females the sex ratio should favor males on study plots where removals occurred. Uterine tracts from adult females killed on these plots were removed and preserved in formalin. The number of embryos was recorded so that actual litter size at emergence could be compared to the predicted litter size based on average embryo count.

Suggestions have been made that adult females may influence the dispersal of juveniles (Goulet and Sadleir, 1974; Michener and Michener, 1977). To test this hypothesis adult females were removed from two study plots after weaning of young. The subsequent loss from and immigration onto these plots were compared to loss from and immigration onto control plots where adult females remained.

The effect of predation on the sex ratio was assessed by comparing the sex ratio of the Richardson's ground squirrels found in hawk nests in the area (data collected in a concurrent study, J. Schmutz, 1977).

Results and Discussion

Population Characteristics of Richardson's Ground Squirrel

In this study of dispersal and mortality it was essential that the populations studied be identifiable as individuals at all times. During the course of this study 1414 Richardson's ground squirrels were individually marked, of which only 872 were considered to be residents of the study plots. These residents were captured a total of 6499 times. I believe virtually all resident squirrels were marked. There is no evidence that trappability of the sexes differed. From maps of study plots on which individual capture sites of squirrels were marked during each trapping period, I was able to determine if a squirrel was not recaptured there subsequently. A marked individual, missed during one trapping period, was rarely trapped there subsequently. The average recapture rate of marked squirrels known to be alive was 99% and 97% per trapping period in 1975 and 1976, respectively.

Density

The total number of adult squirrels present from May to August (Table 1) varied considerably between 1975 and 1976. More adult males and fewer adult females were captured in 1976. Table 2 presents the densities of adults reported in this and other studies. The density recorded at Rochester (Dorrance, 1974) and Hanna are comparable although both are

Table 1. Number of adult Richardson's ground squirrels resident on the six plots between May and August

Plot	Adult Females		Adult Males		Total	
	1975	1976	1975	1976	1975	1976
1	25	18 (11/7)[1]	3	12 (2/10)	28	30
2	13	14 (8/6)	1	1 (1/0)	14	15
3[2]	11	-	2	-	13	-
4[2]	13	-	2	-	15	-
5	27	11 (7/4)	1	6 (2/4)	28	17
6	12	10 (8/2)	1	5 (4/1)	13	15
Total	101	53	10	24	111	77

[1]total (older adults/yearlings)
[2]squirrels were removed from these two plots in 1976

Table 2. Recorded densities of Richardson's ground squirrels

Location	Adults/ha	Year	Size of Study Area	Authority
Rochester Alta.	3.8-7.5	1969	25.9 ha	Dorrance (1974)
	3.7-15.5	1970		
	2.6-19.5	1971		
	0.7-5.5	1972		
Kayville, Sask.	0.9	1969	135 ha	Michener and Michener (1977)
	1.0	1970		
	1.4	1971		
Hanna, Alta.	3.3-7.0	1975	24 ha	This study
	3.8-7.5	1976		

higher than in the Regina study which encompasses a much larger area (Michener and Michener, 1977).

Sex Ratio

Table 3 presents the adult sex ratios reported for Richardson's ground squirrels. There is considerable variation in the sex ratio both spatially and temporally; the ratio may fluctuate radically from one year to the next as in this study and that of Dorrance (1974). When juveniles emerged from the natal burrows, the sex ratio did not differ significantly from 1:1 (Gunderson, 1961; Dorrance, 1974; Michener and Michener, 1977; this study).

Age Structure

The age structure of the population was similar in both years. The juvenile class comprised 74% (308/419) of the population in 1975 and 76% (247/324) in 1976. Michener and Michener (1977) report that juveniles comprised 69-75% of the population.

Yearlings comprised 79% (34/43) of the adult population in 1976. Dorrance (1974) reported that 48-65% of the adult female population was composed of yearling females and 73-86% of adult males were yearlings during the three years of his study. Michener and Michener (1977) report that yearlings composed 46% of the adult population in 1970 and 53% in 1971.

Table 3. Reported adult sex ratios in populations of Richardson's ground squirrels

Location	Males:Females	No. of Adults	Authority
Cass County, N.D.	0:13	13	Quanstrom (1968)
	0:9	9	
	1:7.5	15	
Ministik, Alta.	1:11	12	Wehrell (1979)
	1:17	18	
Youngstown, Alta.	1:3.5	68	Goulet and Sadleir (1974)
	1:3.6	87	
Rochester, Alta.	1:5.7	125	Dorrance (1974)
	1:5.25	331	
	1:19	209	
Kayville, Sask.	1:4.25	126	Michener and Michener (1977)
	1:4.8	145	
	1:2.7	197	
Hanna, Alta.	1:9.9	111	This study
	1:2.2	77	

Natality

Several studies have reported the litter sizes of Richardson's ground squirrels (Table 4). Variability between years occurs in all studies including the present one.

Wehrell (1973) and Dorrance (1974) have suggested that some mortality is suffered between birth and emergence of the young above ground. Therefore embryo counts from squirrels near term or placental scar counts when compared with counts of emerged young, should give an estimate of this mortality. The average embryo count was 5.2 per female among 23 females in 1976. The average litter size was 4.7 (Table 4). Therefore, the average mortality before emergence was 0.5 per litter.

Dorrance (1974) found a significantly greater implantation rate (embryo counts of pregnant females and placental scar counts of postpartum females) among older adults than among yearlings on some study plots but not on others in his study area. However, embryo counts alone showed no significant difference between yearlings (6.40, n=8) and older adults (7.20, n=5). Sheppard (1972) found no significant difference between total embryo counts of yearling (7.44, n=84) and older adult females (7.46, n=41) collected near Regina, Saskatchewan. I removed 16 pregnant females from plots 3 and 4 (Fig. 1) in 1976 and because they were marked from the previous year, I was able to classify them as yearlings or older adults. Total embryo counts

Table 4. Recorded litter sizes from populations of Richardson's ground squirrels

Location	Mean Litter Size	Number of Females	Basis	Authority
Laramie Basin, Wyoming	5.9	69	embryo counts, placental scar counts, young born in captivity	Clark (1970)
Wyoming	6	7	young/ adult female in the lab	Denniston (1957)
Highmore, S.D.	6	8	embryos/ pregnant adult female	Gunderson (1961)
Rochester, Alta.	8.8	84	embryos/ adult female	Nellis (1969)
Edmonton, Alta.	4.2 3.4	11 17	number of emerged young/ adult female	Wehrell (1973)
Youngstown, Alta.	2.1 3.6	34 16	number of emerged young/ adult female	Goulet and Sadleir (1974)
Rochester, Alta.	6.3 5.6 3.7 4.8	105 168 161 16	estimate of young/ estimate of adult females	Dorrance (1974)
Hanna, Alta.	3.0 4.7	101 57	number of emerged young/ adult female	this study

(including resorbing embryos) (Table 5) showed a significantly larger litter size among older adults than among yearlings (Mann-Whitney U=47, P<.05). Therefore the age structure of the female population may also influence the number of young emerging from the burrows.

Loss of Squirrels from Local Populations

Loss includes mortality and emigration. Table 6 records the number of animals marked in 1975 that were still resident on the plots in 1976 and the percentage of animals lost in each class. Although interyear loss is high in all sex and age classes (Table 6), it appears to be more marked in the males within both age classes. However, the rates of loss for the two sexes were not significantly different in either the adult or juvenile age classes. The loss among female adults was significantly less than among female juveniles using a log likelihood ratio test (Sokal and Rohlf, 1969) (G=18.38, P<.05) but the loss among males did not differ significantly among adults and juveniles. Michener and Michener (1977) reported that interyear loss from 1969 to 1970 and from 1970 to 1971 was greatest among juvenile males (97% and 78%), intermediate among juvenile females (79% and 65%) and adult males (75% and 60%), and least among adult females (52% and 48%).

Table 5. Embryo counts from 5 yearling and 11 older adult female Richardson's ground squirrels collected on plots 3 and 4 (Fig. 1) in 1976.

Age of adult female	Mean embryo count	Range
Older Adult (n=11)	5.5	0-7
Yearling (n=5)	4.2	3-5

Table 6. Number of resident Richardson's ground squirrels surviving between 1975 and 1976

Number	Adult		Juvenile	
	Females	Males	Females	Males
Marked in 1975	101	10	138	170
Recaptured in 1976 (%)	45 (45)	4 (40)	25 (18)	19 (11)
Lost (%)	56 (55)	6 (60)	113 (82)	151 (89)

Dispersion

The squirrels are always associated with burrows. Burrows are most often located on "slight knolls of the prairie a few feet above the general level" (Coues, 1875:151). Several advantages accrue: the soil is looser, visibility is increased (Coues, 1875), drainage is better (Quanstrom, 1968), and food is abundant (Bailey, 1926). Therefore because I trapped at burrows and burrows were clumped, the location of squirrels shows a clumped pattern of distribution. Appendices 1-12 illustrate the aggregation of points on the six plots at which animals were trapped during the 2 years of this study.

Hypotheses Concerning Causes of Differential Loss of Males and Females from Local Populations of Richardson's Ground Squirrels

Hypothesis 1: Early Spring Loss

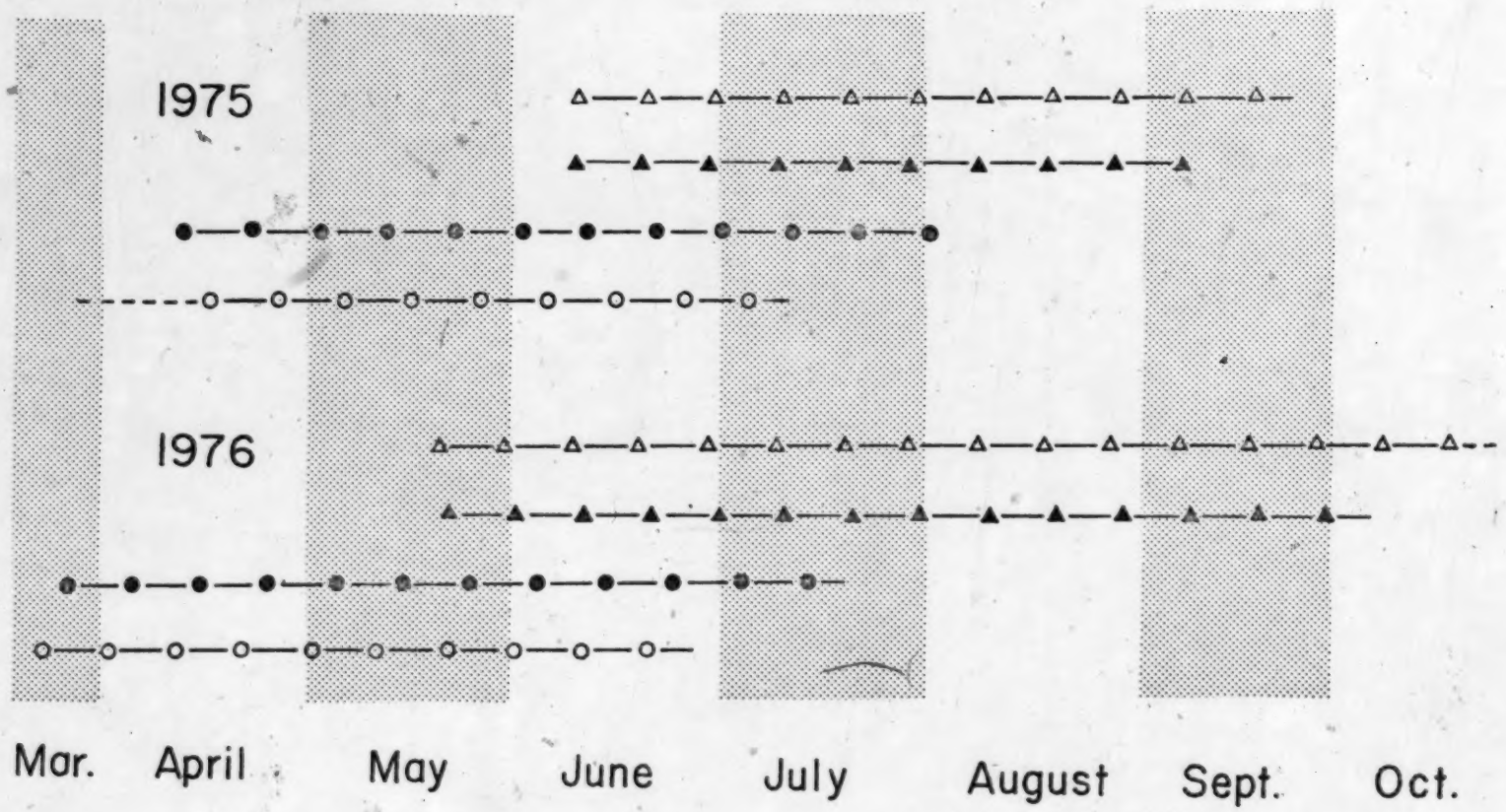
Inclement weather and snow cover are believed to cause mortality among males, especially those males moving outside their home range in early spring (Dorrance, 1974). He found two males dead and stated (p. 52) that "they presumably became lost in the snow". Since these meteorological conditions would affect male ground squirrels for longer periods of time than females, because of the

earlier emergence of males, they may represent a cause of differential mortality.

In 1975, ground squirrels emerged between March 9 and 25; the exact date of emergence was unknown. In 1976, I was constantly in the field from early March onwards and therefore was able to observe and capture males on their first day above ground, March 22 (Fig. 2).

Snow cover in 1975 was still unbroken on March 25 when I returned to the study area and observed ground squirrels for the first time. Although systematic trapping on the plots did not begin until May, sporadic trapping was conducted in April to locate suitable plot locations. Both sexes were captured on April 12 although males predominated (5:1), suggesting that females may only just have begun to emerge. Tracks in the snow were seen to extend 50 to 100 m away from the nearest open burrow. Thus, the possibility for ground squirrels to become disoriented seemed to exist although no evidence of such disorientation was found. In 1976, snow cover was incomplete when the first ground squirrel emerged on the study plots on March 22. Therefore it seems unlikely that any loss recorded at this time could be attributed to snow cover. Nevertheless, predation was recorded during this early postemergence period. On March 22, 1976 snowy owls (Nyctea scandiaca) were observed to kill two Richardson's ground squirrels about 1.5 km from the plots. Since female squirrels had not yet been trapped at this time, I presume these squirrels were males. At this

Figure 2. The maximum period each sex and age class of Richardson's ground squirrels was active above ground on the study area. ●—● Adult females, ○—○ adult males, ▲—▲ juvenile females, △—△ Juvenile males.


1975
1976
Mar.
April
May
June
July
August
Sept.
Oct.

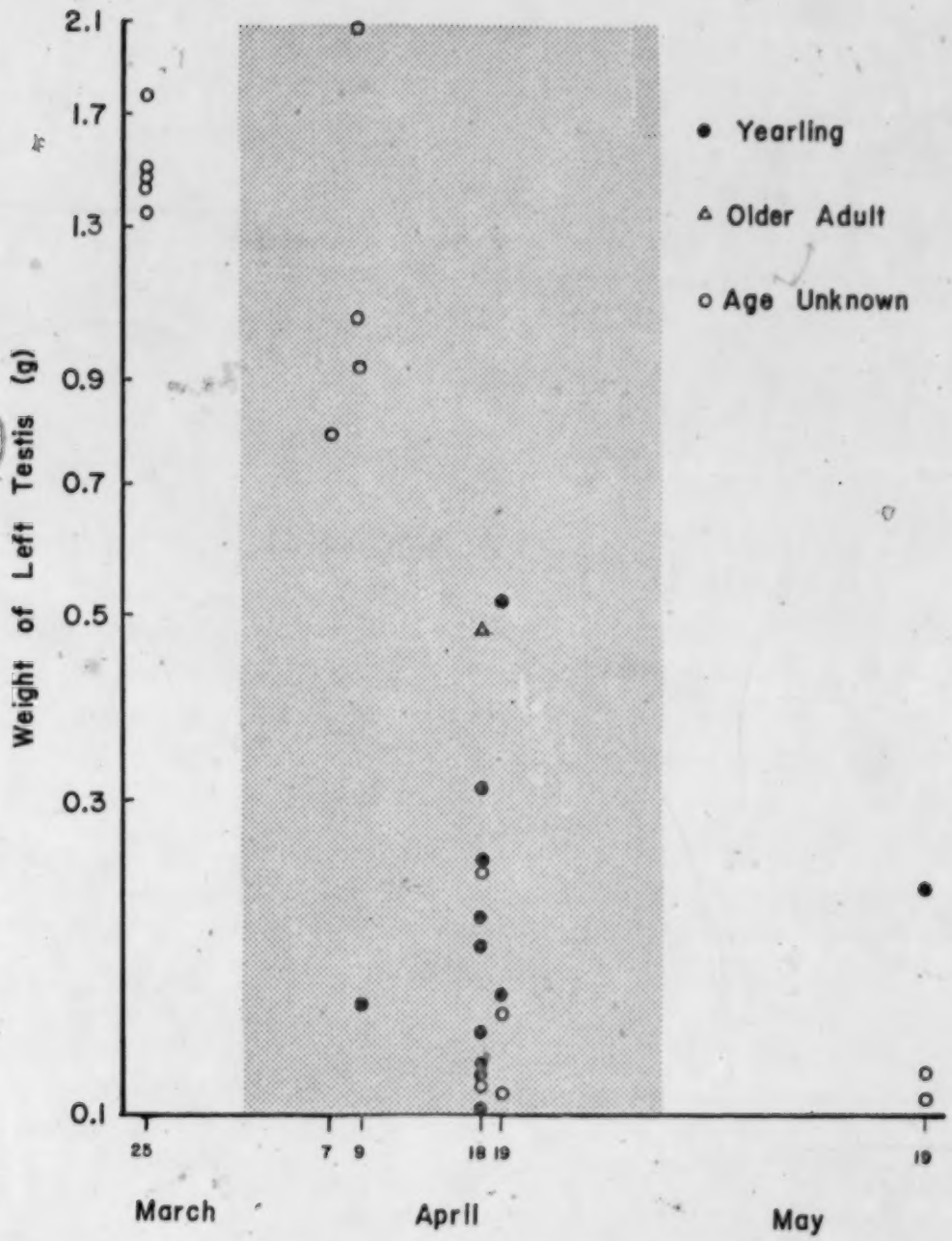
time, ground squirrels are conspicuous against patches of snow which often remained near burrow mounds. Thus it is conceivable that this segment of the squirrel population was vulnerable to predation pressure from avian predators, particularly migrating buteonine hawks known to pass through the area in large numbers at this time of year (personal observation). Since raptors feed during migration (Cochran, 1975), this influx of avian predators could exert a high predation pressure on the relatively small proportion of the total ground squirrel population which had just emerged from hibernation. The aspect of predation will be discussed in greater detail in a later section. Since it is highly probable that some mortality occurred before females emerged, loss during this period through death must contribute to upsetting the sex ratio among adults in favor of females.

Such loss should be evident in recapture rates of squirrels during this period. The rate of loss during March was greater among males than females. Five of 10 adult males (50%) trapped in March were absent in April whereas only 3 of 12 females (25%) were absent. This loss could have been due to either emigration or mortality or both.

Movements, that may include dispersal, seem to be extensive at this time and may be related to the period of peak breeding. Breeding begins within 2 weeks after emergence of the females (Gunderson, 1961; Quanstrom, 1968; Nellis, 1969; Yeaton, 1972; Dorrance, 1974). Such would

seem to be the case on this study area also. One female was collected on April 5 and seven on April 7, 1976. Embryos were visible in 6 of the 8 uteri. Therefore breeding had occurred prior to April 5. Between March 25 and April 18, 26 males, from which the left testis was removed, were collected. Gunderson (1961) reported that at the time of emergence testes were enlarged and descended. Weight of testis, which is correlated with sperm production in Richardson's ground squirrel (Clark, 1970), was relatively high on March 25 (Fig. 3) but by April 19 had diminished greatly. This also suggests that most breeding probably was completed by April 9. Yeaton (1972) and Michener and Michener (1977) assumed that the sex ratio was already disparate at the time of breeding, and hence reasoned that each male must breed more than one female since almost all females become pregnant (Nellis, 1969; Sheppard, 1972; Wehrell, 1973; Dorrance, 1974; D. Michener, 1974). Michener and Michener (1977) assessed the average female home range to be about 150 m long and that therefore a male would have to move about 450 m to breed three females. D. Michener (1972:41) stated that "[p]roportionally, the greatest wanderers were adult males." Yeaton (1972) stated that male territories included the burrows of three to five females and were approximately three times as large. These data suggest that males probably move over greater distances than females.

Figure 3. The weight of the left testis of male Richardson's ground squirrels (log scale) during and after the breeding season in 1976.


2.1
1.7
1.3
0.9
0.7
0.5
0.3
0.1
Weight of Left Testis (g)
Yearling
Older Adult
Age Unknown
25
7
9
18
19
19
March
April
May

To determine whether males moved over greater distances than females on the study area, I recorded distances from one capture point to the next from time of emergence until April 19 (Fig. 4). The mean distance moved by adult males was significantly greater than by adult females (Student's $T=-3.91$, $P<.01$, log transformation).

Since I believe that all resident squirrels were marked on the plots in 1975, any unmarked squirrels trapped in 1976 were considered immigrants. In March and April, 1976 I caught 18 unmarked males and 5 unmarked females. This suggests that more males than females were dispersing at this time. Dorrance (1974) reported similar findings; 16 males and 6 females that he caught in April on a 24.3 ha area were unmarked. Michener and Michener (1977) attribute most movement of adult males to the spring period and report that the proportion of unmarked males to unmarked females was higher than in the marked population, suggesting that more males immigrated into the population than females.

As an additional measure of dispersal among adults, all squirrels were removed from plots 3 and 4 (Fig. 1) on April 18 and 19, 1976; this included 17 males and 19 females (Table 7). Subsequently, 6 males and 10 females immigrated onto these plots. These data suggest that immigration after April 19 was proportional to the numbers of each sex available in the surrounding population. Females comprised 64% of the surrounding populations and they formed 62.5% of the immigrants onto these plots. It would appear,

Figure 4. Movement of adult Richardson's ground squirrels from time of emergence to April 19, 1976, based on 158 recaptures of males and 77 recaptures of females. Mean and one standard error shown.

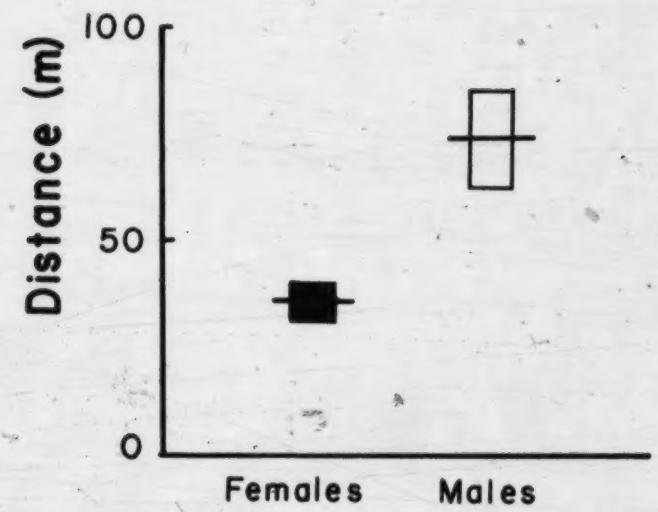

Distance (m)
100
50
0
Females
Males

Table 7. Numbers of adult Richardson's ground squirrels that recolonized plots 3 and 4 after removal of original residents

Plot	Removed April 18-19		Removed May 19-21		Present June-July	
	Females	Males	Females	Males	Females	Males
3	8	4	2	2	1	1
4	11	10	8	4	2	0
Total	19	14	10	6	3	1

therefore, that any differential movement by the sexes had ceased by April 19. Between May 19 and 21 all immigrant squirrels on these plots were again removed. It is noteworthy that most of the immigrant females had been pregnant. The number of each sex of adults that immigrated after this second removal (Table 7) suggest that the same proportions are maintained between the sexes. Dorrance (1974) removed only adult males from a 4.2 hectare area before April 16 and found no immigrant males subsequently. However he did record unmarked males, presumably immigrants, that entered other parts of his study area during April.

Fighting among males has been suggested as another cause of mortality in Richardson's ground squirrels (Dorrance, pers. comm.) and ground squirrels (Steiner, 1970, 1972). Although some wounding was observed in male Richardson's ground squirrels in this study, it apparently was never of a serious nature. Some fighting and chasing was observed that involved both males and females, but never of an intensity that would have resulted in mortality. Therefore it seems unlikely that fighting caused differential loss in Richardson's ground squirrels.

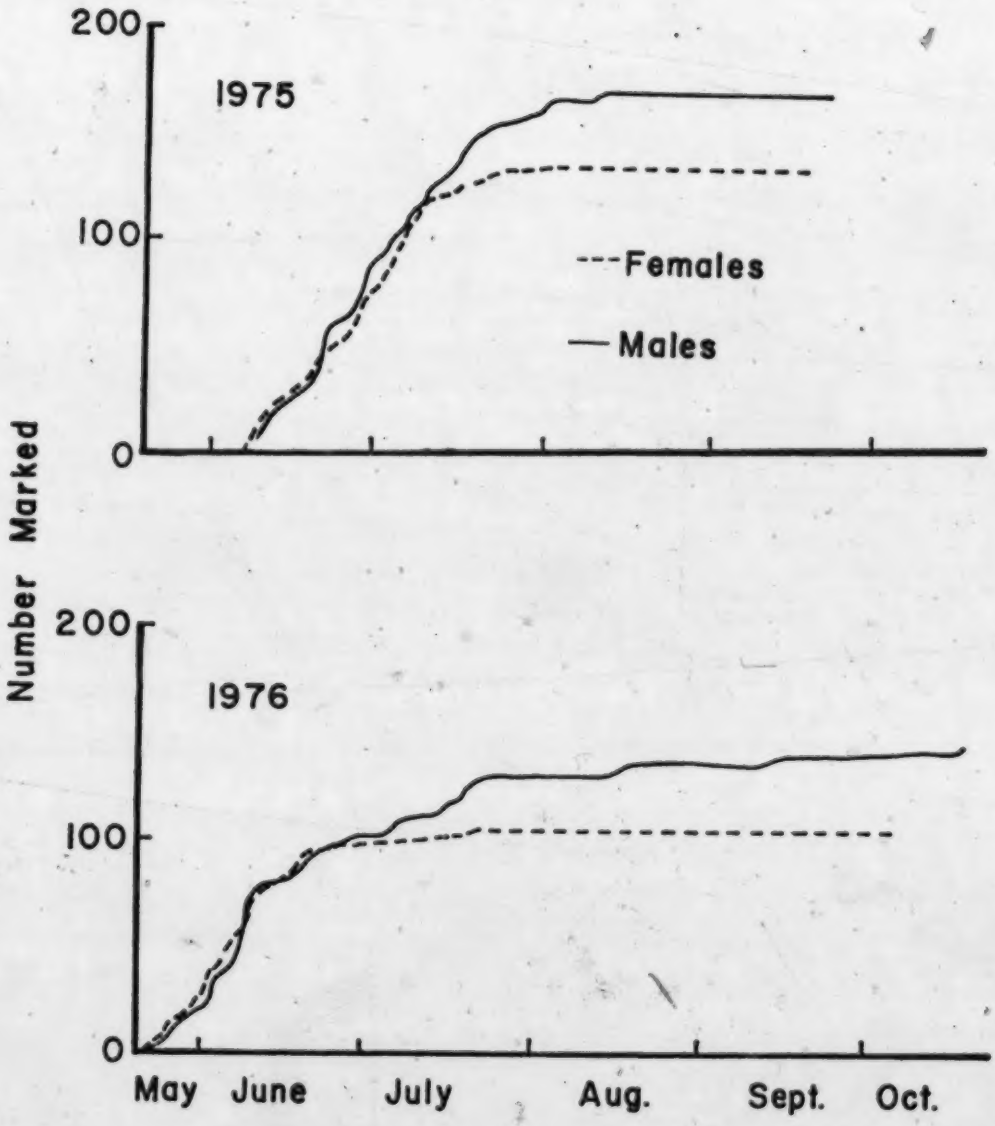
In summary, evidence suggests that during the spring period, from emergence to mid-April, the loss of overwintered males probably exceeds that of females. Although adverse weather conditions were not shown to have a

demonstrable effect snow cover appears to increase the chances of predation and since males are exposed to snow cover longer than females, it affects them more. Fewer males than females trapped in March were still present in April. Movements of males in March and April were longer than females and more males than females immigrated onto the plots at this time. These data suggest that males may be more vulnerable than females tc predation because of these movements and that they may also be moving

Hypothesis 2: Juvenile Dispersal and Mortality

Juveniles first emerged from the natal burrows on the study plots on June 9 in 1975 and on May 21 in 1976 (Fig. 2). Figure 5 presents the cumulative number of juveniles marked over time in the 2 years. The data from 1975 are from all six plots, however the data from 1976 are only from plots 1, 2, 5, and 6, the plots on which squirrels were born. For the first month post-emergence in both years the cumulative number of marked males was approximately equal to that of marked females. Thereafter the number of males continued to increase, although at a much slower rate, whereas the number of females did not increase appreciably after this time. The ratio of the final number of juvenile males and females marked on the plots deviates from equality

Figure 5. The cumulative number of juvenile Richardson's ground squirrels marked on the plots in 1975 and 1976.


200
1975
100
---Females
—Males
0
Number Marked
200
1976
100
0
May
June
July
Aug.
Sept.
Oct.

in 1975 ($X^2=3.34$, $P<.10$) and in 1976 ($X^2=5.54$, $P<.05$). Since Richardson's ground squirrels have been found repeatedly to have a 1:1 sex ratio at birth (Gunderson, 1961; Nellis, 1969; Michener and Michener, 1971; Sheppard, 1972; D. Michener, 1974) and in this population in the first month after emergence (Fig. 5), this unbalanced sex ratio after 1 month cannot be attributed to an unbalanced sex ratio at birth. Therefore the only possible explanations are that either females were being lost from the populations on the plots more rapidly than males during the first month or that males were dispersing more than females and as a consequence were appearing as immigrants to the population in greater numbers than females. I did not find that more females than males were lost during the first month post-emergence. Although Yeaton (1969) observed disappearance of juveniles from litters 7 to 10 days after emergence, with most disappearing before 1 month (June 29), he implies more males disappeared than females. Therefore the most plausible explanation for the data presented in Fig. 5 appears to be that males are dispersing more than females beginning approximately one month after emergence.

The resident juvenile population during each prehibernation month is presented in Table 8. The sex ratio is never significantly different from 1:1 in any month. This supports the hypothesis that although more males were marked, more males were steadily lost.

Table 8. Number of juvenile Richardson's ground squirrels present each month

	May		June		July		August	
Year	Females	Males	Females	Males	Females	Males	Females	Males
1975	-	-	65	75	112	119	48	59
1976	6	8	92	93	73	83	47	54

Quanstrom (1971) described juvenile movements as gradually increasing in distance from the natal burrow during the first month above ground. G. Michener (1973) stated that juveniles remained near the burrow after emergence but (p. 37) "[a]fter 2-3 weeks they were moving over the area used by the mother." At the end of one month "several" animals were seen more than 150 m away (Quanstrom, 1968). He observed one animal 1.6 km away and shot another (a juvenile male) 9.6 km away. Quanstrom (1968:51) further states that "[d]uring these first two weeks of July it was common to see young squirrels several miles from the nearest colony." He records that 33 of 35 road-killed juveniles were males. Although he was not able to determine the sex of animals observed at considerable distances, the road-kill data suggest males were moving more than females. This description of behavior is compatible with a differential dispersal of juvenile males 1 month after emergence.

A similar increase in movement of juveniles about 1 month after emergence was noted by Wehrell (1973). She stated that juveniles disappeared during the fourth week after emergence. Juveniles continued to disappear from her study area during the following month, July, but at a much slower rate.

Dorrance (1974) stated that no juvenile immigrants were found before late June, 3 to 4 weeks after emergence of juveniles. He also stated that immigration was negligible after mid-July since marked to unmarked ratios of juveniles

did not change. Dorrance (1974) concluded that immigration occurred in late June and early July. Males (76%) predominated among immigrants in July in all 3 years of his study. Also more males than females disappeared between June and July.

If more males are dispersing than females, emigration as well as immigration among males should exceed that of females. Although emigration can not be separated from mortality in calculations of loss, mortality "in situ" is probably equal between the sexes. Assuming equal "in situ" mortality rates, differential loss must result from differential emigration. Figures 6 and 7 are graphic presentations of the numbers of juveniles present on each plot in each trapping period of 1975 and 1976 and the percentage loss and percentage gain from one trapping period to the next. Trapping periods were staggered among plots but occurred at approximately one-month intervals on each plot. The proportion of juveniles lost from 1 month to another on all the plots is also presented in Figs. 6 and 7. Although time intervals vary, they were the same for both sexes on each plot so that a relative proportion can be calculated. Male loss exceeded female loss from June to July but loss was relatively equal between the sexes from July to August. The loss of females from August to September probably included some entrance into hibernation. Michener and Michener (1977) state that hibernation of juveniles begins in early September with females usually

Figure 6. Number of juveniles present during each trapping period in 1975, rate of loss since the previous trapping period and rate of gain in terms of immigrants. Cross hatching, stippling, etc. indicate unmarked animals trapped for the first time. The designation of the bars remains constant for the duration of the animal's residence on the plots. The rate of loss is the percentage of marked squirrels that were lost since the previous month. The rate of gain is the percentage of squirrels captured for the first time in that month. No rate of gain is shown for July because all squirrels born on the plots had not been marked in the previous month.

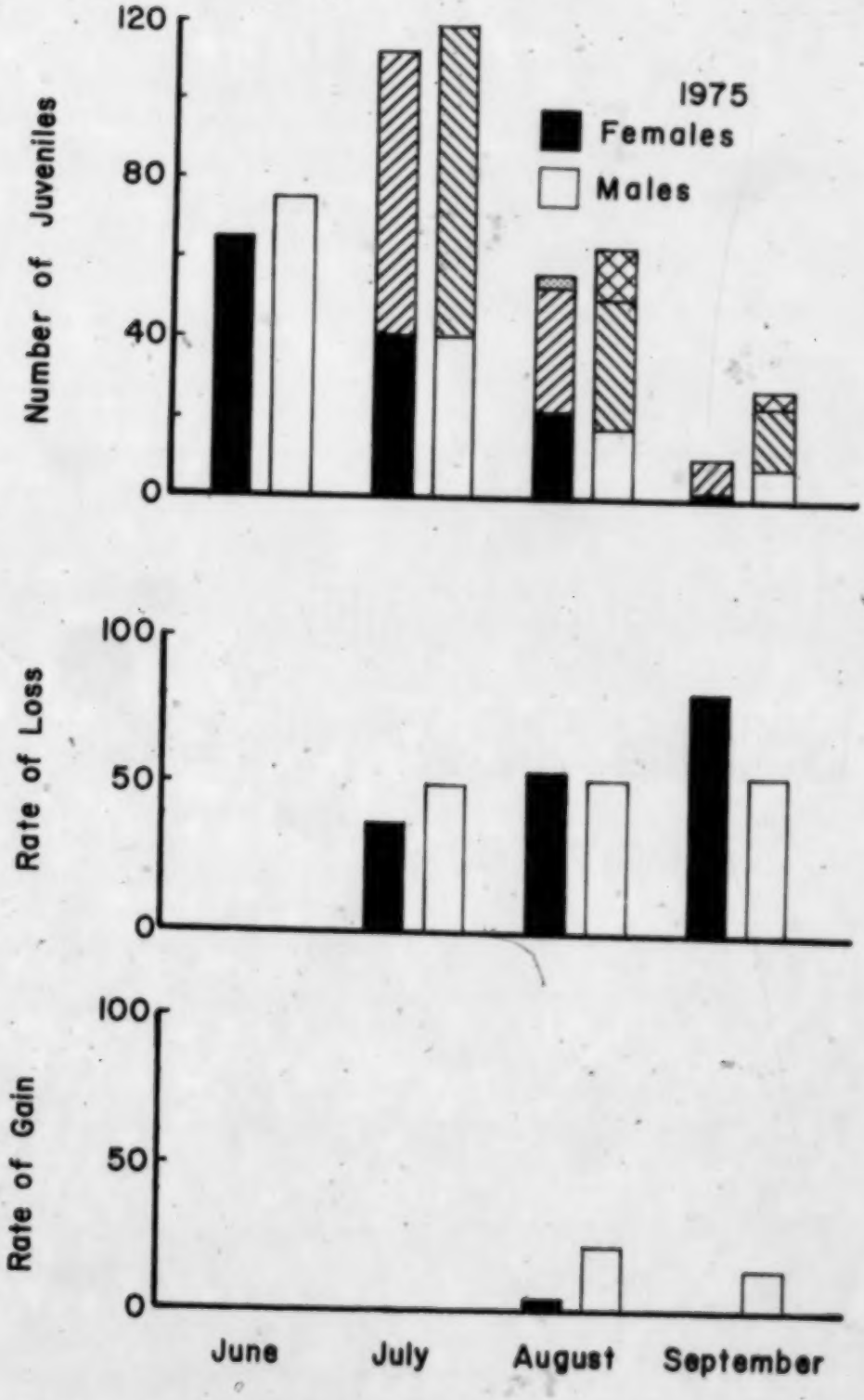
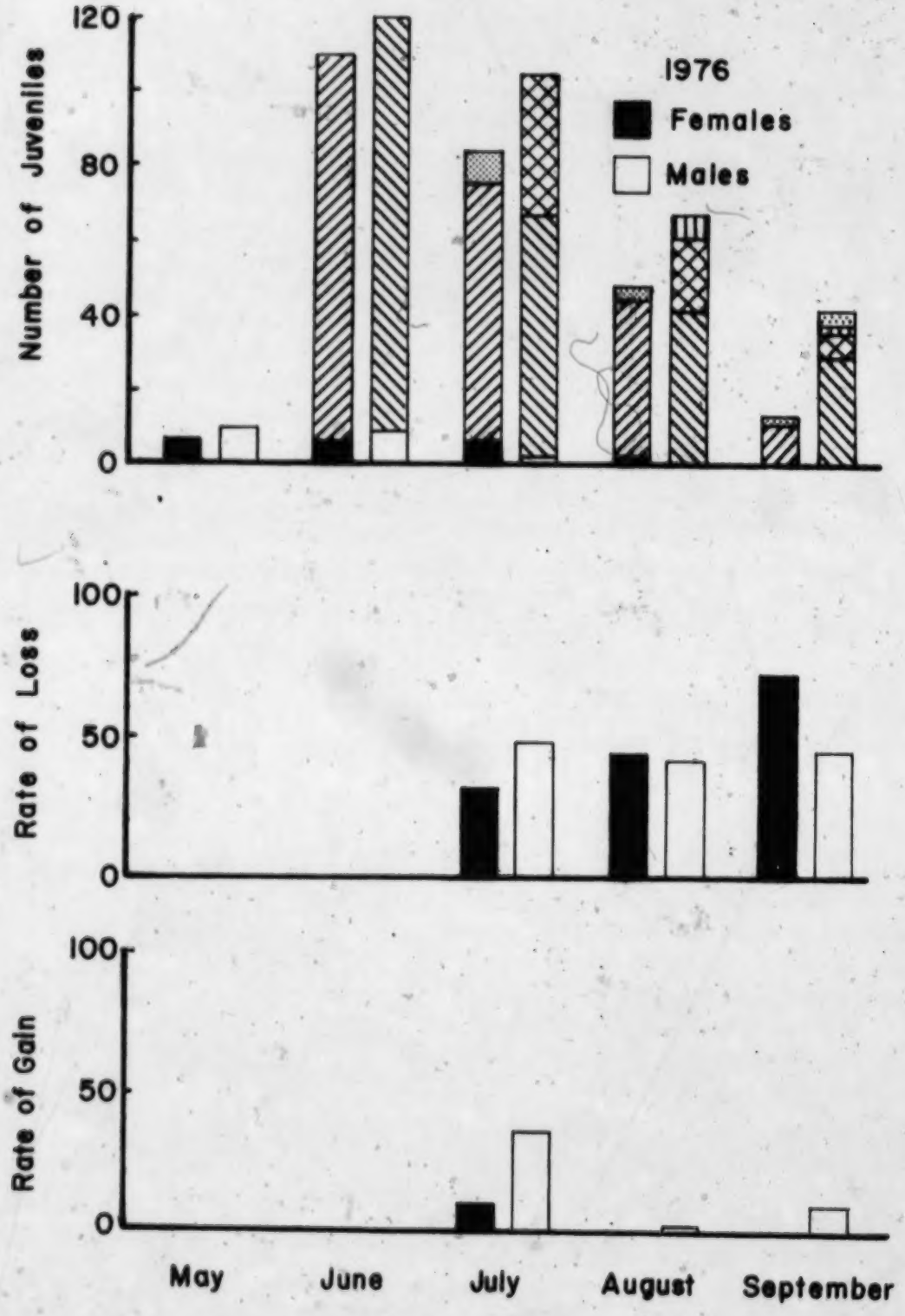

120
80
40
0
Number of Juveniles
1975
Females
Males
100
50
0
Rate of Loss
100
50
0
Rate of Gain
June
July
August
September

Figure 7. Number of juveniles present during each trapping period in 1976, rate of loss since the previous trapping period and rate of gain in terms of immigrants. Cross hatching, stippling, etc. indicate unmarked animals trapped for the first time. The designation of the bars remains constant for the duration of the animal's residence on the plots. The rate of loss is the percentage of marked squirrels that were lost since the previcus month. The rate of gain is the percentage of squirrels captured for the first time in that month. No rate of gain is shown for June because all squirrels born on the plots had not been marked in the previous month.


120
80
40
0
Number of Juveniles
1976
Females
Males
100
50
0
Rate of Loss
100
50
0
Rate of Gain
May
June
July
August
September

entering hibernation before males. Males appear to emigrate in greater numbers than females. The number of unmarked males exceeds the number of unmarked females, indicating more male immigration. This immigration does not compensate for the greater loss among juvenile males however. Yeaton (1969) recorded a ratio of three males to one female among 12 juvenile immigrants.

An additional experiment was undertaken to record relative rates of immigration of juveniles by removing all adults from plots 3 and 4 (Fig. 1) before the young emerged (May 21, 1976). These plots were trapped for an additional 2-3 days after the removal of adult females. All juveniles trapped during this period were also removed. Therefore all juveniles recorded on these plots thereafter were immigrants. More males than females moved onto plot 3 (21:10) and plot 4 (14:11) (X^2=3.5 [combined data], $P<.10$) which also suggests that male dispersal exceeds that of females.

Suggestions have been made in the literature that adult female aggression may prevent juveniles from establishing on their territories (Goulet and Sadleir, 1974). G. Michener and Sheppard (1972:1348) stated "adult females tend to ignore and reject (though not aggressively) their own male young, at the same time engaging in more neutral and cohesive contacts with their female young." They suggest a possible relationship between this differential social behavior and dispersal of juveniles. To test the effect of

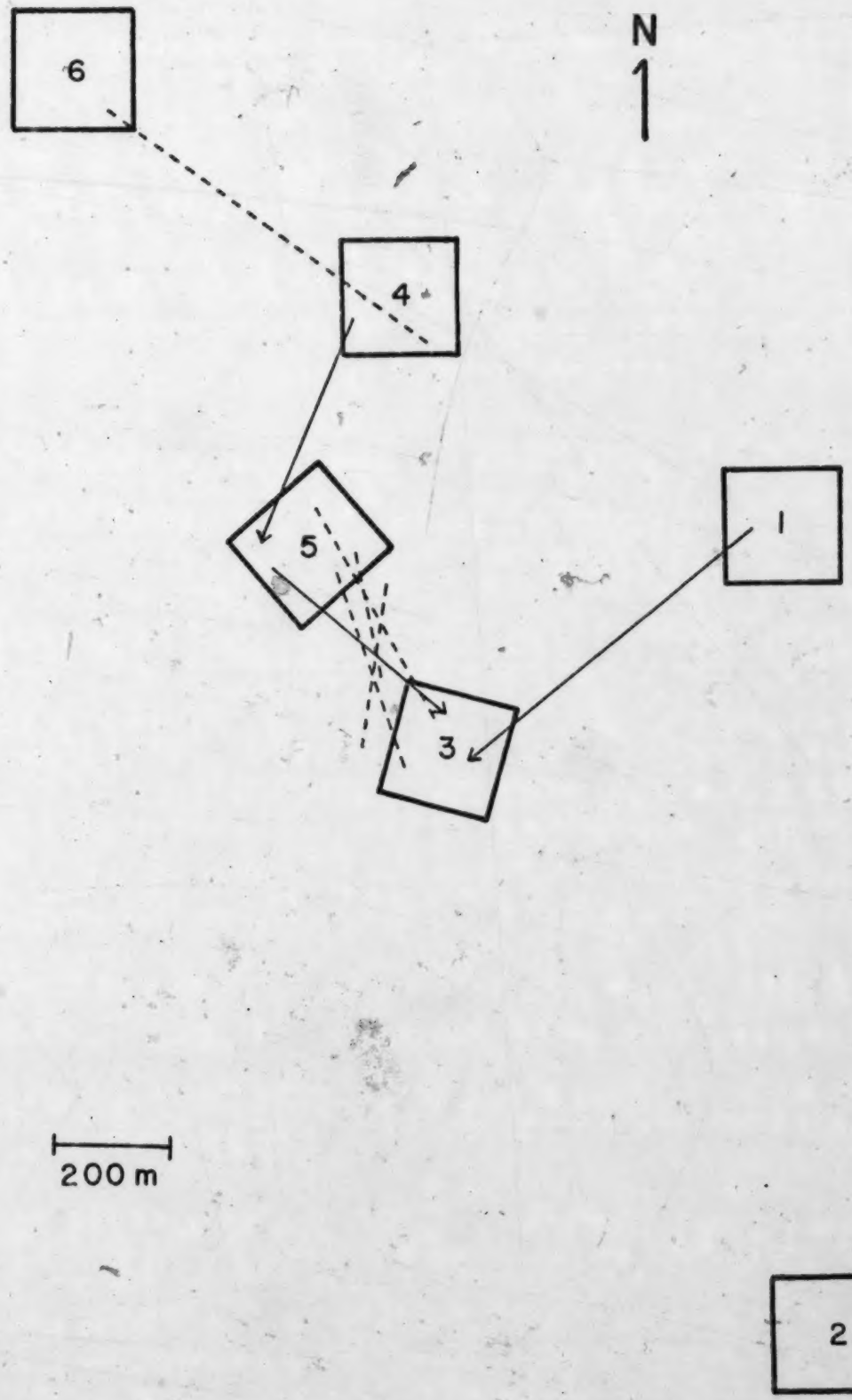
adult females on juvenile immigration and emigration, adult females were removed from plots 2 and 6 (Fig. 1) during the first week of July at a time when the young were essentially independent. If adult females were influencing dispersal patterns in the young, the pattern of dispersal from these plots would differ from those plots on which adult females remained. The sex ratios on plots where adult females were removed (Table 9, plots 2 and 6) did not differ from those on unmanipulated plots (Table 9, plots 1 and 5). Furthermore, the ratio of juvenile males to females was not significantly different between 1975 and 1976 on these manipulated plots. This suggests that adult females were not influencing relative rates of emigration and immigration during the time period considered.

If juvenile males are moving either more often or over greater distances than females, the number of interplot movements by marked males should exceed that of marked females. The distance between study plots ranged from 0.18 km to 2.15 km (Fig. 1). Late in 1975 one juvenile male moved from plot 5 to 3, a distance of 500 m. In 1976 it was present again on plot 5. In 1976, movements between five of the six plots were recorded (Fig. 8). All movements recorded for juveniles were made by males. Although movements probably radiate out in all directions from each plot, I caught only those animals moving between plots or their buffer zones, and thus the apparent directionality of the movements in Figure 8 is an artifact of the areas

Table 9. Number of juvenile Richardson's ground squirrels resident during 1975 and 1976 on the plots on which squirrels were born

	1975		1976	
Plot	Females	Males	Females	Males
1	38	37	37	56
2	23	32	26	34
3	8	12	-	-
4	15	22	-	-
5	40	42	24	27
6	14	25	18	25

Figure 8. Movements made by juvenile males between plots in 1976. Broken lines indicate back and forth movements. Solid lines indicate one way movements.


N
6
4
5
1
3
2
200 m

trapped. Furthermcre these recapture data probably underestimate the number cf long distance movements yet do not overestimate the proportion of these movements made by juvenile males.

Greater juvenile male than juvenile female dispersal is indicated by these data. Differential dispersal would not alter the sex ratio if immigration equaled emigration because gain would compensate for loss. If immigration and emigration are not equal, differential dispersal may change sex ratios locally however dispersal alone can not alter the sex ratio of the populaticn as a whole. Differential mortality associated with dispersal is necessary to alter the sex ratio of the whole population. It appears that interyear loss is greater among immigrants than among squirrels born and remaining on the plots, assuming all juveniles marked before July 12, 1975 were natives and all after, were immigrants (Table 10). A G test indicated that there was no significant difference between number still present and number lcst amcng natives and immigrants for females (G=0.232), but there was a significant difference (G=4.91, P<.05) for males. Since male dispersal is greater than female dispersal even a small reduction in the chances of survival of immigrants may affect the sex ratio.

In summary juvenile males appear to leave the sites of their birth in greater numbers than juvenile females. The sex ratio during the first month after emergence remained 1:1 but subsequently as more males entered the population

Table 10. Survival among native and immigrant juvenile Richardson's ground squirrels between 1975 and 1976.

	Juvenile Females		Juvenile Males	
	Natives	Immigrants	Natives	Immigrants
1975	121	17	124	46
1976	23	2	18	1

through immigration than females, the total number of each sex marked departed from equality (Fig. 5) even though resident populations maintained a 1:1 ratio. Between June and July more males than females were lost from each plot. The presence of adult females on the plots did not appear to affect rates of loss or immigration among juveniles of either sex. Among juveniles, all recorded movements between plots were made by males. Interyear loss of juveniles was greater, although significantly so only for juvenile males, among immigrants than among squirrels born on the plots. Therefore since more immigrants are males, this sex suffers more interyear loss.

Hypothesis 3: Predation

Predation is a possible factor causing a disparate sex ratio among Richardson's ground squirrels. If this is the case, a predator must selectively take more of one sex than the other.

It was difficult to separate dispersal and mortality in most aspects of this study. Predation is a mortality factor but may be related to dispersal because it may be during the dispersal phases that squirrels are more vulnerable to predation. This is an important consideration because increased male dispersal alone would not upset the sex ratio if emigration equaled immigration as commonly assumed.

Suggestions have been made that dispersing individuals are more subject to predation than sedentary individuals (Metzgar, 1967). He found that screech owls (Otus asio) selectively preyed upon transient rather than resident mice in a laboratory study. Intuitively, these results would be expected because an animal in unfamiliar territory presumably would find escape more difficult. Snyder et al. (1976) demonstrated that a ferruginous hawk killed mice that were unfamiliar with their surroundings significantly more often than mice that were familiar with their surroundings in a laboratory situation and attributed this to greater activity of the selected group. However unfamiliarity with surroundings pertains primarily to animals in the process of dispersing since an immigrant presumably would become familiar very rapidly with its surroundings.

A dispersing squirrel would also be at a disadvantage if it were forced into peripheral, less suitable habitat (Klomp, 1972). An animal may immigrate into a sparsely populated area which may not be optimal for breeding (Murray, 1967; Smith, 1974). An important requirement for ground squirrel survival seems to be the availability of suitable burrows (Shaw, 1926; Quanstrom, 1968) not only to avoid predators but also to survive generally. Similarly talus has been reported to be important for pikas (Ochotona princeps) (Smith, 1974). Smith (1974) suggests that during dispersal pikas are most vulnerable to predation because at

this time they are often away from talus. Thus, if appropriate burrows are not available to dispersing ground squirrels, they may be more vulnerable to predators during these movements.

Richardson's ground squirrels are preyed upon by both avian and mammalian predators. Isolated cases of predation on Richardson's ground squirrels by feral house cats (Felis domesticus) (Quanstrom, 1968), weasels (Mustela sp.) (D. Michener, 1972; Wehrell, 1973; Dorrance, 1974), badgers (Taxidea taxus), (Clark, 1970; Wang, 1973) raptors (Clark, 1970), and mink (Mustela vison) (Dorrance, 1974) have been reported. Attempts at predation by coyotes (Canis latrans), red-tailed hawks (Buteo jamaicensis) (Wehrell, 1973), and skunks (Mephitis mephitis) (Quanstrom, 1968) have been observed also.

Sheppard and Swanson (1976) analyzed feces of mammalian predators collected during June and July over 3 years in an area where Richardson's ground squirrels were being studied (D. Michener, 1972). Of the 92 feces of badger, red fox (Vulpes fulva), and long-tailed weasel (Mustela frenata) 38 (41%) contained Richardson's ground squirrel remains.

Richardson's ground squirrels have been estimated to compose a large percentage of the items in the diets of many raptors. Enderson (1964) found Richardson's ground squirrels to be a major prey item of prairie falcons (Falco mexicanus). Several studies of red-tailed hawks report Richardson's ground squirrels constituting a significant

part of the diet: 13-25% (Luttich et al., 1970), 13-32% (McInvaille and Keith, 1974), and 49-74% (J. Schmutz, 1977). In the vicinity of the plots studied (Fig. 1) Richardson's ground squirrels composed 67-72% of all items found in the nests of Swainson's hawks (Buteo swainsoni) and 85-93% of food items in the nests of ferruginous hawks (Buteo regalis) (J. Schmutz, 1977). Burrowing owls (Speotyto cunicularia) (Seton, 1929) and great horned owls (Bubo virginianus) have also been reported to prey on Richardson's ground squirrels occasionally (McInvaille and Keith, 1974).

Many of these potential predators were present on the study area. Coyotes, badgers, long-tailed weasels, and skunks were observed. Harriers (Circus cyaneus), ferruginous hawks, Swainson's hawks, red-tailed hawks, rough-legged hawks (Buteo lagopus), snowy owls, prairie falcons, and golden eagles (Aquila chrysaetos) were also seen at some time during which ground squirrels were active above ground. Although actual cases of predation by these animals were rarely observed, they may have considerable impact. One badger was seen in the area carrying a young Richardson's ground squirrel. Two juveniles were found dead on a study plot, bitten in the neck, possibly by long-tailed weasels, two of which were captured on the same plot that day. Harriers were common and are capable of capturing and killing ground squirrels (Bailey, 1926). In 1975, a Richardson's ground squirrel (probably an adult since young

had not yet emerged) was observed killed, after a brief struggle, by a harrier. In 1976 an adult male harrier was flushed with a squirrel in his talons that was subsequently retrieved and proved to be a juvenile male weighing about 200 g.

A concurrent study of prey taken by two resident hawk species during the nestling period indicated that Richardson's ground squirrels are the major prey item (J. Schmutz, 1977). Both ferruginous and Swainson's hawks nested in relatively high densities on the study area as well as in the general vicinity. In Fig. 1 the location of the nests closest to the study plots is shown. On July 17, 1975 one marked juvenile male was found in a ferruginous hawk nest approximately 1.6 km east of its last capture site (June 27) on plot 2 (Fig. 1). On June 17, 1976 one marked adult female was found in the ferruginous hawk nest 0.68 km east of its last capture site (May 27) in the buffer area of plot 3.

Although a quantitative assessment of predation on the study plots can not be made a qualitative assessment of the relative impact on ground squirrel sex and age classes can. Table 11 summarizes the total numbers of ground squirrels found primarily in 14 Ferruginous and 12 Swainson's Hawk nests in 1975 and 1976. The nests were visited daily for approximately 8 weeks. The total number of adult males:adult females in the prey did not differ significantly from the ratio in the study population (Table 1), based on

Table 11. Number of Richardson's ground squirrels found in raptor nests on and around the study area in 1975 and 1976

	Adults		Juveniles	
Year	Females	Males	Females	Males
1975	47	10	262	312
1976	20	7	191	323
Total	67	17	453	635

Chi-Square tests, in either year during the study. It does not appear that raptor predation during the summer period alters the adult sex ratio. It is noteworthy that although adult males were relatively scarce they did appear as prey. Juvenile males were taken more frequently than juvenile females. The prey ratio of juveniles killed varies significantly from the ratio of juveniles at birth, 1:1, in 1975 (χ^2=4.07, P<.05) and in 1976 (χ^2=33.03, P<.01). It therefore appears that juvenile males were preyed upon disproportionately to their numbers in the population. Increased rates and distances of dispersal may make males more vulnerable to predation. Snyder (1975) suggested that increased activity and weight in some cases, may also increase chances of predation. He tested the responses of a red-tailed hawk to active versus inactive (drugged) prey and to large versus small prey. He found that active prey were chosen over inactive. I did not collect activity data other than movement and therefore cannot comment on the applicability of Snyder's findings to this study.

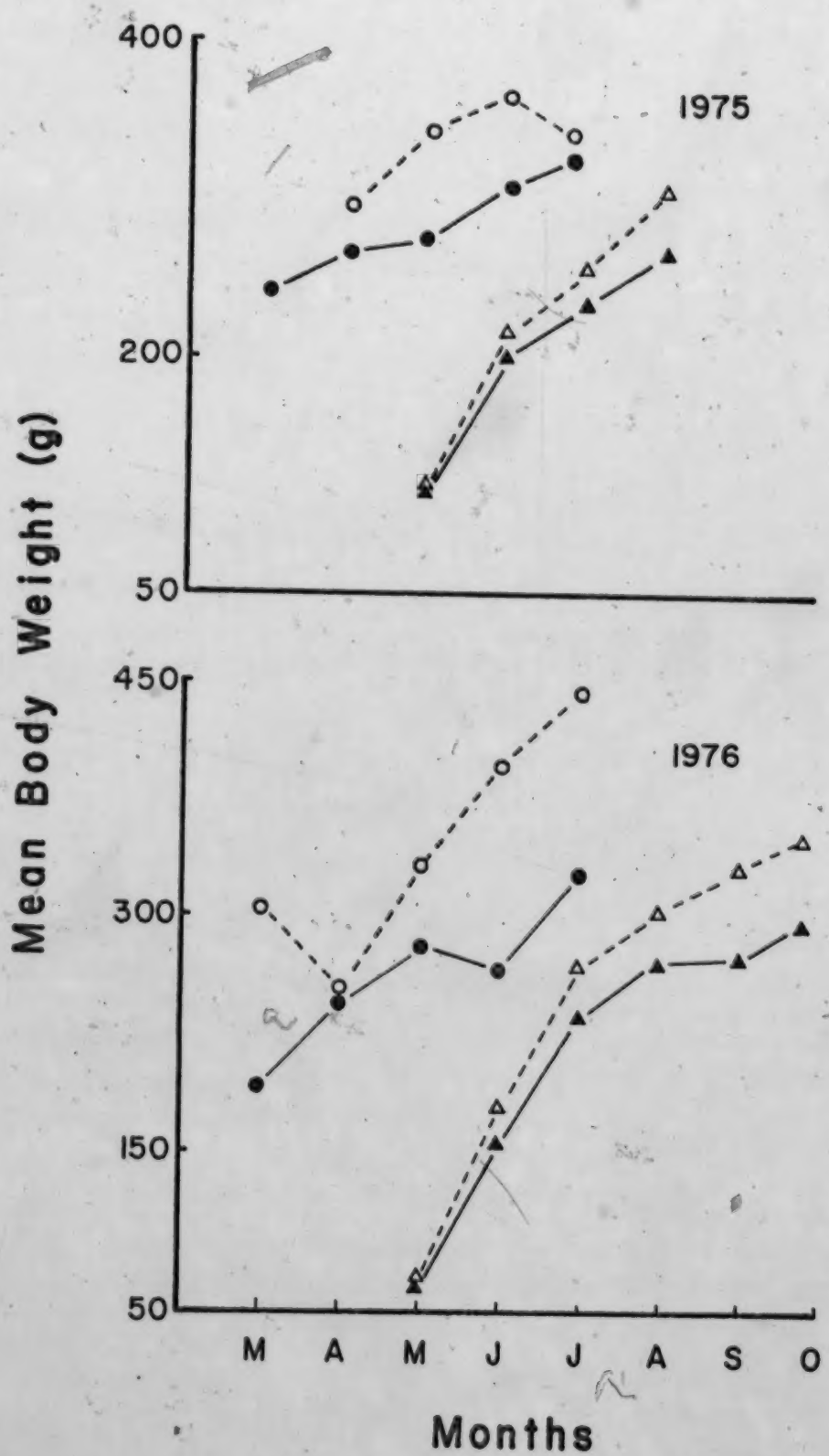
Snyder (1975) found that larger prey were preferred over smaller prey by a red-tailed hawk. The larger prey were at least 55 g heavier than the small prey in his experiments which meant that the large prey was twice as heavy as the small prey in some cases. D. Michener (1974) demonstrated that for the first 2 weeks juvenile weights did not differ, but thereafter juvenile male weights exceeded those of juvenile females. He also demonstrated that mean

weights of adult males exceeded those of adult females. Mean differences on a weekly basis were never found to exceed 48.4 g (D. Michener, 1974). Dorrance (1974) also presented data indicating that males weigh more than females. Figure 9 illustrates that males were heavier than females in any given month in both age classes in this study, even during the period of female pregnancy. If predators can detect such weight differences, then greater weights of males may influence their chances of predation if other variables such as availability and wariness are equal.

Only one other study of predation on Richardson's ground squirrels reports sex ratios of prey (Luttich et al., 1970). They report that, among juveniles found at red-tailed hawk nests the ratios "were similar to" 1:1. They also stated that adult males composed 57% of adult prey but only 12% of the trapped population in the same area. These data were based on a series of extrapolations for which the explanation of derivations was insufficient to make comparisons with data obtained at ferruginous and Swainson's hawk nests in this study.

Luttich et al. (1970) stated that 23-34% of the loss from the ground squirrel population resulted from red-tailed hawk predation, yet Dorrance (1974) assessed this predation to be of minor importance to the ground squirrel population. Dorrance (1974) studied Richardson's ground squirrels in the vicinity of the study area used by Luttich et al. (1970). He reported that less than 2% of marked juvenile

Figure 9. Mean body weight of each sex and age class of Richardson's ground squirrels on the study area. ●—● Adult females, O--O adult males, ▲—▲ juvenile females, Δ--Δ juvenile males.


400
200
50
1975
450
300
150
50
1976
Mean Body Weight (g)
M A M J J A S O
Months

Richardson's ground squirrels and only two marked adults were found at these red-tailed hawk nests.

Early spring and late autumn are times when densities of predators are greatest with the annual migration. For example in March of 1976, 101 sightings of raptors which prey on Richardson's ground squirrels were recorded on the study area (52 snowy owls, 27 ferruginous hawks, 11 rough-legged hawks, 1 red-tailed hawk, 4 golden eagles, 6 harriers). Swainson's hawks entered the area in April. A similar passage of raptors through the area occurs in September and October. Snowy owls may not enter the area until November however. Therefore many avian predators are in the area when only males are active, increasing mortality rates among them. The last trapping round began on August 25 in 1975. Twelve of the 35 males (34.2%) present after that time and 8 of the 15 females (53.3%) survived until the next spring ($G=0.88$, $P>.05$). This may be the time when the major contribution of predation to the disparate sex ratio is made.

In summary, avian predation appears to remove more males than females, probably because males are more vulnerable through their greater movements. The greatest impact on the sex ratio probably occurs during late summer when juvenile males are dispersing in greater numbers than females and predators are feeding their young. Additional predation pressure is placed on males in autumn and again in spring when only males are active.

Hypothesis 4: Overwinter Mortality

Overwinter mortality has been suggested as a means of altering the sex ratio of Richardson's ground squirrels (Michener and Michener, 1977). Any estimate of overwinter mortality must include mortality that occurs in late autumn since animals that emerge the following spring have entered hibernation over a period of 1 month. All mortality can not be attributed to the above-ground period, suggesting that overwinter mortality does occur. The extent of this overwinter mortality cannot be determined at this time but there is no reason to believe that it was different between the sexes. Table 12 presents an estimate of maximum loss among adults between June, the last month Loss among juveniles was calculated from July 12 to the following spring in order that only squirrels born on the plots be included in the estimate. It appears that loss was not markedly different between the sexes during this period. Therefore, although loss is high, the overwinter period probably does not account for differential loss. Dorrance (1974) also found that loss of adults from May to the following spring did not differ markedly between the sexes.

Loss of animals between years (Table 6) indicated that more, although not significantly more, males were lost within each age class. This loss could occur during the hibernation or above-ground period. Differential loss

Table 12. Maximum overwinter survival of Richardson's ground squirrels on the plots.

Age and Sex	Number Alive		Loss (%)
Adult	June 1975	Spring 1976	
Females	86	45	48
Males	8	4	50
Juveniles	July 12, 1975	Spring 1976	
Females	121	23	83
Males	124	18	85

between the sexes during the above-ground period apparently explains most of this differential interyear loss. It appears that most estimates of overwinter mortality are calculated from the date the first surviving individual disappeared to hibernate until the first individual emerged the following year. This would include at least one month when other members of the particular sex-age class were still above ground daily and not yet hibernating. Thus above-ground losses are not clearly differentiated from below-ground losses in these records of annual loss.

Dorrance (1974) calculated overwinter mortality rates for juveniles from August, when surviving individuals began to disappear, to the following spring. This calculation includes some loss during the above-ground period and is therefore not overwinter mortality only. He suggested that the greater loss suffered by juvenile males can be explained by loss during the 2 to 3 weeks when only males were above ground in autumn based on rates of loss in previous months. D. Michener (1974) and Dorrance (1974) found a tendency for higher survival among those individuals with higher prehibernation weights, within each sex and age class. They further suggested that heavier animals may enter hibernation before lighter individuals of the same sex and age class because the mean weight of active animals declined shortly before the end of the above-ground period. Wehrell (1973) reported that heavier females, such as those which lost litters, entered hibernation sooner. It would therefore

appear that heavier animals are below ground for longer periods of time since they enter hibernation sooner. This may negate any advantage imparted by increased prehibernation weight.

Overwinter mortality may be related to period spent below ground. Table 13 summarizes the dates each sex and age class was last and first seen above ground. The period spent below ground is a minimum estimate since it is based on observations of any one individual within each sex and age class. Since squirrels within each sex and age class are believed to differ in times of entrance into hibernation, perhaps by more than a month (Wehrell, 1973; Dorrance, 1974; Goulet and Sadleir, 1974; Michener and Michener, 1977) and to emerge over a 2-week period (Clark, 1970; Wehrell, 1973), there could be considerable overlap of amount of time spent under ground among the sex and age classes. Thus the correlation between survival and time spent hibernating is difficult to imagine.

D. Michener (1974) also reported that juvenile males spend the shortest average time below ground, followed by juvenile females, adult females, and finally adult males that spend the longest time below ground. Since juvenile males spend the least amount of time below ground and yet suffer the greatest loss from one year to the next, it does not seem likely that the underground period is responsible for the greater loss suffered by juvenile males.

Table 13. Dates each sex and age class of Richardson's ground squirrels were observed for the last time in 1975 and the first time in 1976 and the minimum period spent below ground

	Last Observed 1975	First Observed 1976	Period Below Ground
Adult Males	July 12	March 22	253
Adult Females	Aug. 4	March 25	235
Juvenile Females	Sept. 9	March 28	200
Juvenile Males	Sept. 25	March 26	182

The importance of hibernation burrows to the ground squirrel has been suggested by several authors (Quanstrom, 1968; Yeaton, 1969; Michener and Michener, 1977). Michener and Michener (1977) suggest that the number of suitable burrows may be limited and that males may have less chance of using previously proven burrows. They further state that juvenile males may have the least choice because they enter hibernation last. This argument presumes that juveniles do not establish territories which would include a hibernation burrow. If juveniles do establish territories, the date they enter hibernation should not be of consequence since they would possess a hibernation burrow as part of their territory even before they occupied it as such. Yeaton (1972) stated that juveniles defend specific areas against litter mates as well as other young by the end of July. It appears that hibernation burrows may be claimed as part of territories at this time before any juveniles have entered hibernation. If so, juvenile females would not necessarily gain more suitable burrows because they hibernate earlier.

Sheppard and Swanson (1976) studied skeletal remains found at Richardson's ground squirrel burrows and suggest that these remains represent overwinter mortality. Bones of squirrels less than one year of age comprised 76% (n=72) of the identifiable bones whereas juveniles comprised an average of 66% (n=1359, range 61-75%) of the live population. Since Sheppard and Swanson (1976) assumed these disinterred remains represented overwinter mortality they

suggested that underground mortality is disproportionately high on juveniles when compared to adults. They suggest a difference in suitability of hibernacula as a possible explanation of this differential mortality among the age classes. Although this evidence seems to indicate greater juvenile than adult overwinter mortality, the live population was composed of 62% juveniles in 1970 and 120 of 189 (63%) were yearlings the following spring. Therefore the prediction that greater overwinter mortality occurred among juveniles based on the skeletal remains is not supported by survival data from the live population in that year.

Although overwinter mortality exists, I do not believe the evidence in support of a differential overwinter mortality based on sex is conclusive. Neither differences in weight, length of hibernation period, or assumed availability of hibernacula are consistently correlated with overwinter survival differences among the sex and age classes. Much differential loss between years can be explained by differential loss during the above-ground period. Late autumn to spring (overwinter) mortality estimates still include the period of 2 to 3 weeks when only males are above ground. I agree with Dorrance (1974) that loss during these periods probably explains any difference in survival rates of the two sexes.

Summary of Hypotheses Concerning Differential Loss of Sexes

There appears to be no single factor nor time period when the sex ratio in Richardson's ground squirrels is displaced from equality. I examined four hypotheses in which possible explanations for the unequal sex ratio are suggested to affect the sex ratio. An integration of at least two hypotheses is necessary to explain loss in a single sex and age class and an integration of all hypotheses except overwinter mortality is necessary to explain the disparate sex ratio observed.

Periods of approximately 2 weeks in spring and again in autumn when only males were active above ground, appear to be the times when much of the differential loss occurs. Harsh weather conditions and the difficulty of locating burrows in the snow are adverse conditions in the spring which may enhance vulnerability to predation or death from exposure. Migration of avian predators during spring and autumn results in an influx of predators that also increases the predation pressure on males alone.

Differences in rates and distances of dispersal between male and female juveniles have been demonstrated. Although an unequal balance between immigration and emigration would change sex ratios locally, dispersal alone is not sufficient to explain an overall difference in the sex ratio of the population unless accompanied by death during the dispersal movement. Immigrants have reduced survival chances and evidence suggests dispersers in general suffer greater

mortality, presumably mainly through predation. Therefore an emigrant has a higher probability of mortality, even after settling in a new area as an immigrant, than a resident. Thus, immigration is generally lower than emigration and therefore dispersal does affect the sex ratio, although indirectly.

Overwinter mortality appears to be an important factor in year-to-year survival of Richardson's ground squirrels. Overwinter mortality probably accounts for most of the mortality in adults between June and the succeeding spring. There is no evidence that overwinter mortality removes more of one sex than the other. Thus the differential sex ratio apparent in the population must be the result of mortality factors removing more males than females during the above-ground period.

Theoretical Implications of Sex Differential Loss

The causes of the differential sex ratio in Richardson's ground squirrel have been discussed. One can ask why the sex ratio at birth remains equal if it is consistently altered after that time. According to Fisher's principle, the sex ratio at birth remains in equilibrium if the cost of producing the sexes is equal (Hamilton, 1967). Leigh (1970) demonstrated that an allele for equal division of energy input into the production of male and female offspring is always favored, even when differential

mortality between the sexes occurs after the period of parental care.

Therefore since natural selection apparently favors an equal sex ratio at birth, one is forced to consider advantages of an alteration in sex ratio after the period of parental care. Myers and Krebs (1971:325) stated that "[v]ariation in sex ratio may have consequences for population regulation as well as evolutionary theory, and consequently attempts should be made to analyze sex ratios in natural populations".

Trivers (1972) proposed a model which helps to explain the selective advantage of an unequal sex ratio in favor of females. In species with little parental investment in the offspring by the males, the reproductive success of a male rises rapidly if he is able to outcompete other males in inseminating females. To be a successful competitor, a male must have special characteristics such as size, aggressiveness, or mobility. However, the possession of these same characteristics that increase the individual's chances of successful mating, also may increase its chance of mortality.

Male Richardson's ground squirrels are very mobile according to the data presented and thereby are presumed to be able to breed more than one female; this mobility in turn increases their risk of mortality. The risk is nevertheless worth taking because the compensation derived from increased reproductive success is so great. Trivers (1972:155) also

stated "where a male can achieve very high RS [reproductive success] in a breeding season, differential mortality will be correspondingly high." This model fits the data for adult male Richardson's ground squirrels very well, if the stated assumptions are valid, but does not explain differential loss among the juveniles.

Howard (1960) proposed that a tendency to disperse could be genetically sex-linked. He particularly discussed the inheritance of such a trait in "innate dispersers", those individuals which moved beyond their parents' home range, usually at puberty. This perhaps explains the tendency of juvenile male Richardson's ground squirrels to disperse at higher frequencies and over greater distances than females during their first summer. It is this differential movement among the sexes of juveniles that apparently leads to the differential mortality imposed on the males.

Howard (1960) defined "environmental dispersers" as individuals which dispersed in response to density and that a tendency towards this form of dispersal may also be inherited. He suggested that dispersers have a higher risk of mortality than non-dispersers, a suggestion that is supported by this study. A differential dispersal of the type seen in Richardson's ground squirrels has implications for population regulation. If males respond first or more often to increased density on the local level, the population level will decrease locally after a male exodus

but will remain lower only if immigrants are prevented from entering in equal numbers. Since immigrants are subjected to heavier losses than residents, it follows that before such emigrants can become immigrants elsewhere their numbers will be reduced. Thus emigration may exceed immigration and would tend to achieve the lowering of density on a local level. Furthermore the loss of males in a promiscuous species such as Richardson's ground squirrels will have a much smaller impact on subsequent population performance than would a similar loss of females.

Practical Implications for Management of Richardson's Ground Squirrels as a Pest Species

The removal experiments conducted during this study on four of the plots gave some insight into the problems associated with the control of Richardson's ground squirrels on agricultural lands. The results of these particular experiments and this study in general suggest that these squirrels are resilient to periodic removals, at least of the scale undertaken here. The creation of vacant habitat through destruction of local populations provides a vacuum which squirrels rapidly enter through dispersal. The efficiency of campaigns to rid agricultural lands of these mammals must take into consideration the rate of dispersal as well as the distance over which the dispersing squirrels are moving at given times of the year.

If animals are removed very early in the year, before or during the breeding season, effort is probably wasted because many females are still below ground and males are moving over long distances. Repopulation of a 4 ha plot, to former levels, occurred in less than 1 month in this study. Removal of animals is likely to be most effective after the young are born but before they emerge from natal burrows. Because the young are dependent on their mothers at this time, removal of adult females effectively kills juveniles in the burrows as well. Removal experiments at this time indicated that repopulation of the 4 ha plots was considerably reduced.

Juveniles from surrounding areas repopulated the vacant plots to levels comparable to unmanipulated plots, shortly after emergence. Therefore animals must be removed a second time. I did not remove juveniles and therefore can not determine how quickly juvenile repopulation would occur. Immigration onto study plots continued into September so that I would predict some repopulation by juveniles if a second removal occurred before this time. The longest movement, about 884 m, was made by a juvenile male between July 15 and 27, 1976. Quanstrom (1971) recorded a movement made by a juvenile male of 9.6 km. Dorrance (1974) recorded a movement of a juvenile of 3.2 km. Therefore juveniles could move considerable distances to repopulate a vacant area.

Since the results reported here suggest that dispersing individuals may be very vulnerable to predation, every effort should be made to retain predators near areas on which control is conducted. Data collected by J. Schmutz (1977) and Fyfe and Armbruster (unpublished data) suggest that raptors accept artificial nest sites. Erection of nesting structures, placement of baskets in trees, planting of shelterbelts or even single trees near fields where ground squirrel control is in operation should increase the raptor population locally and thereby delay repopulation of fields by immigrant squirrels.

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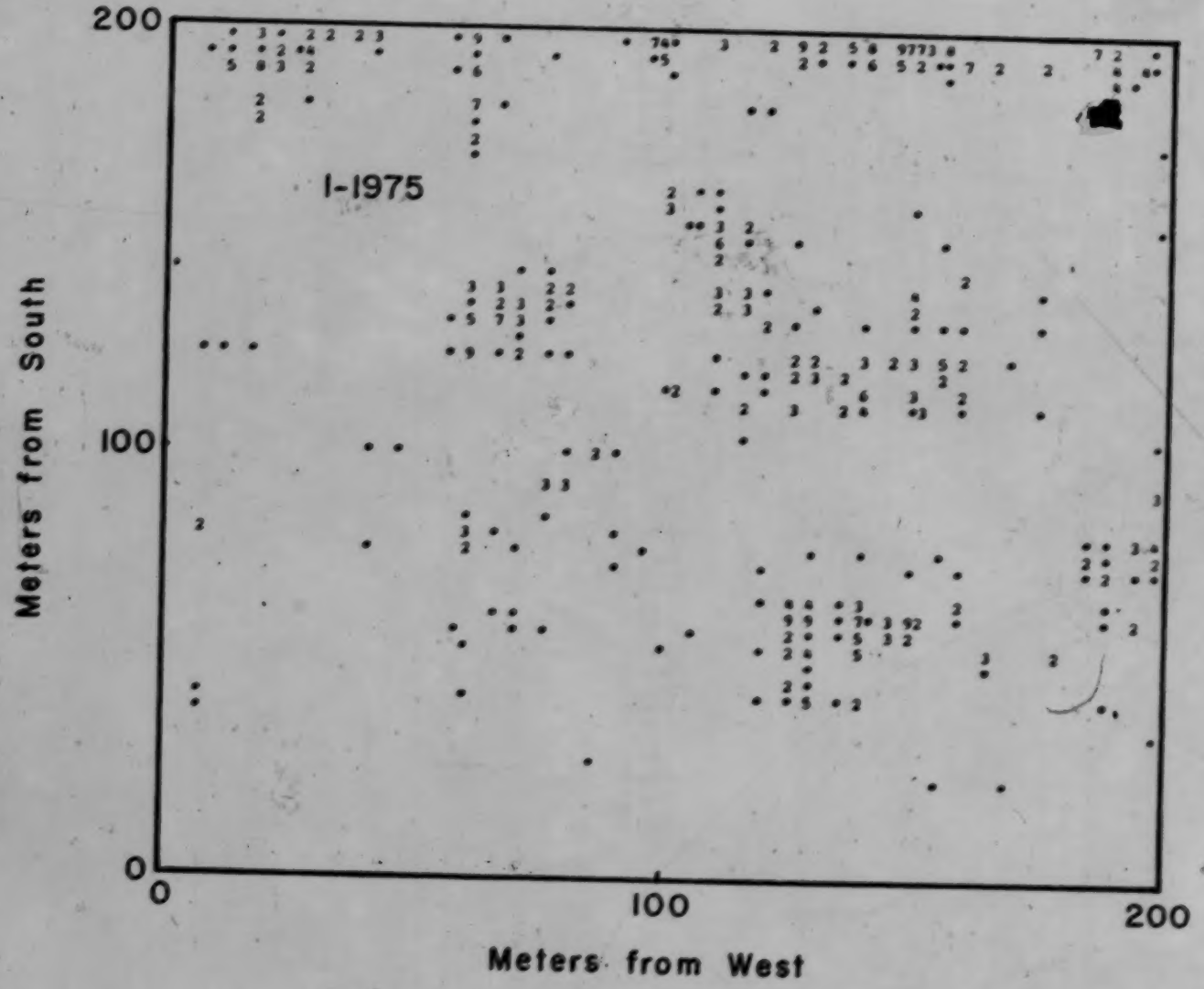
Appendix 1. Dispersion of capture points on plots 1-6 in 1975 and 1976. Several captures at one location are designated by numbers.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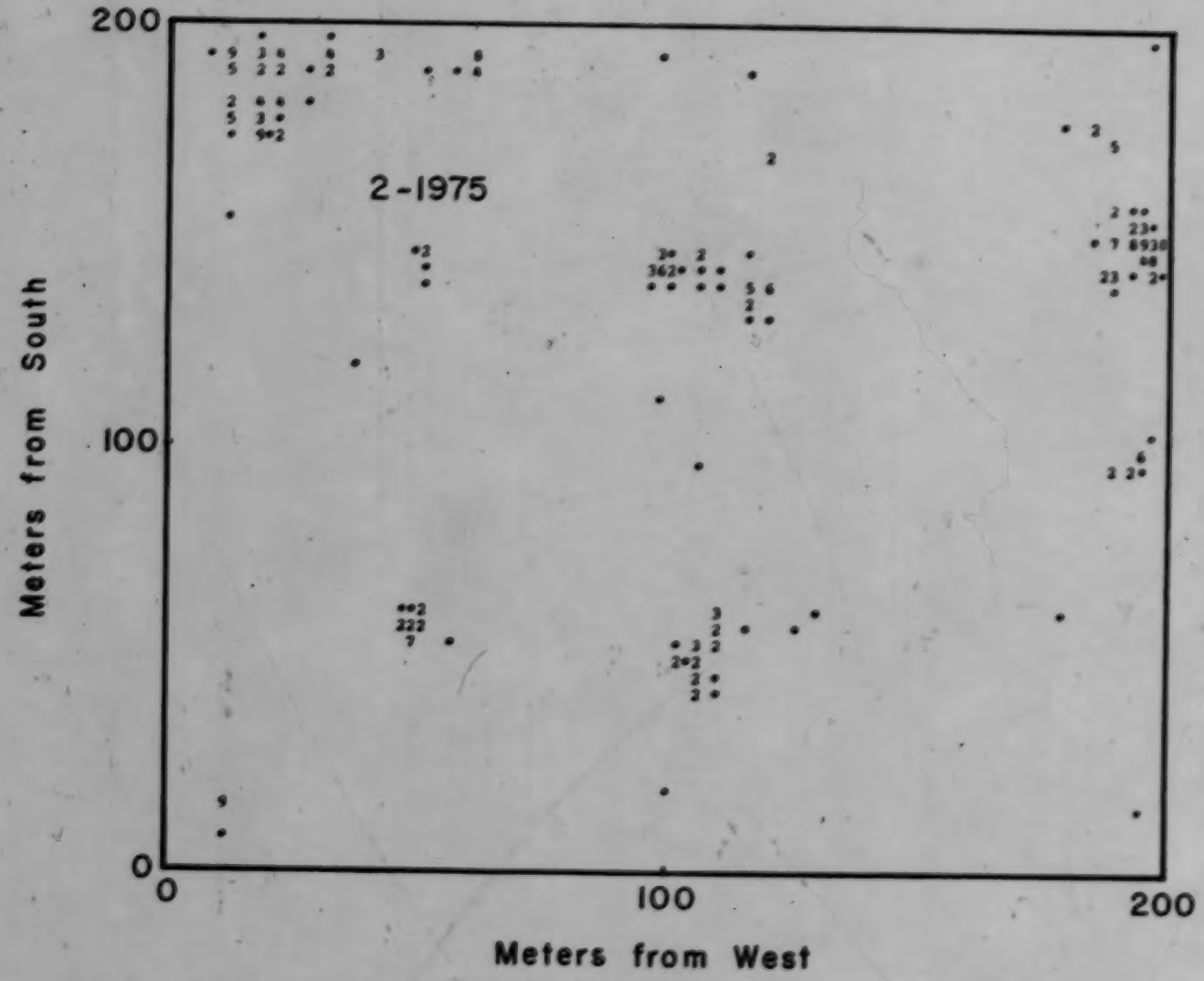
0
0
100
200
Meters from South
Meters from West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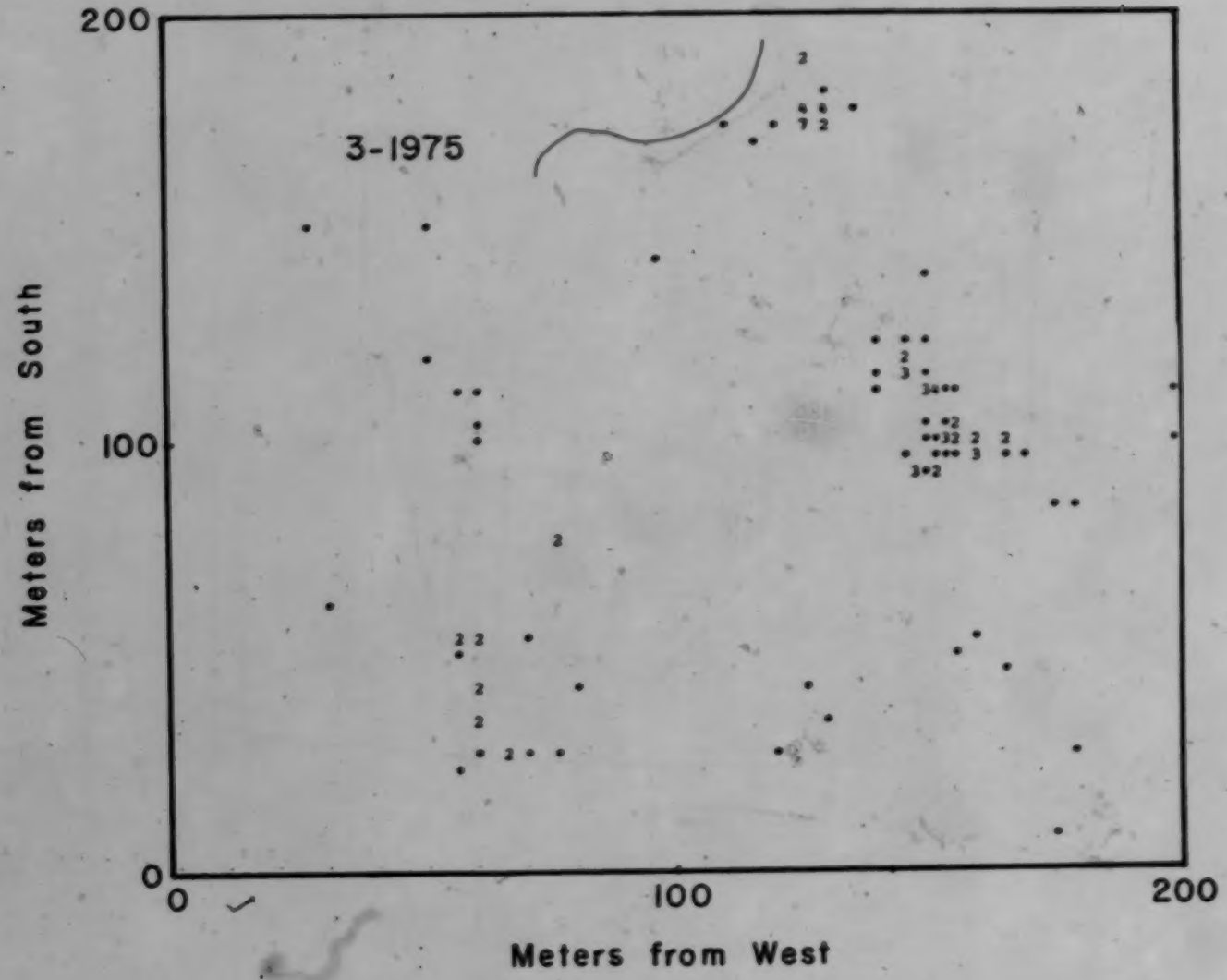
100
0
0
100
200
Meters from South
Meters from West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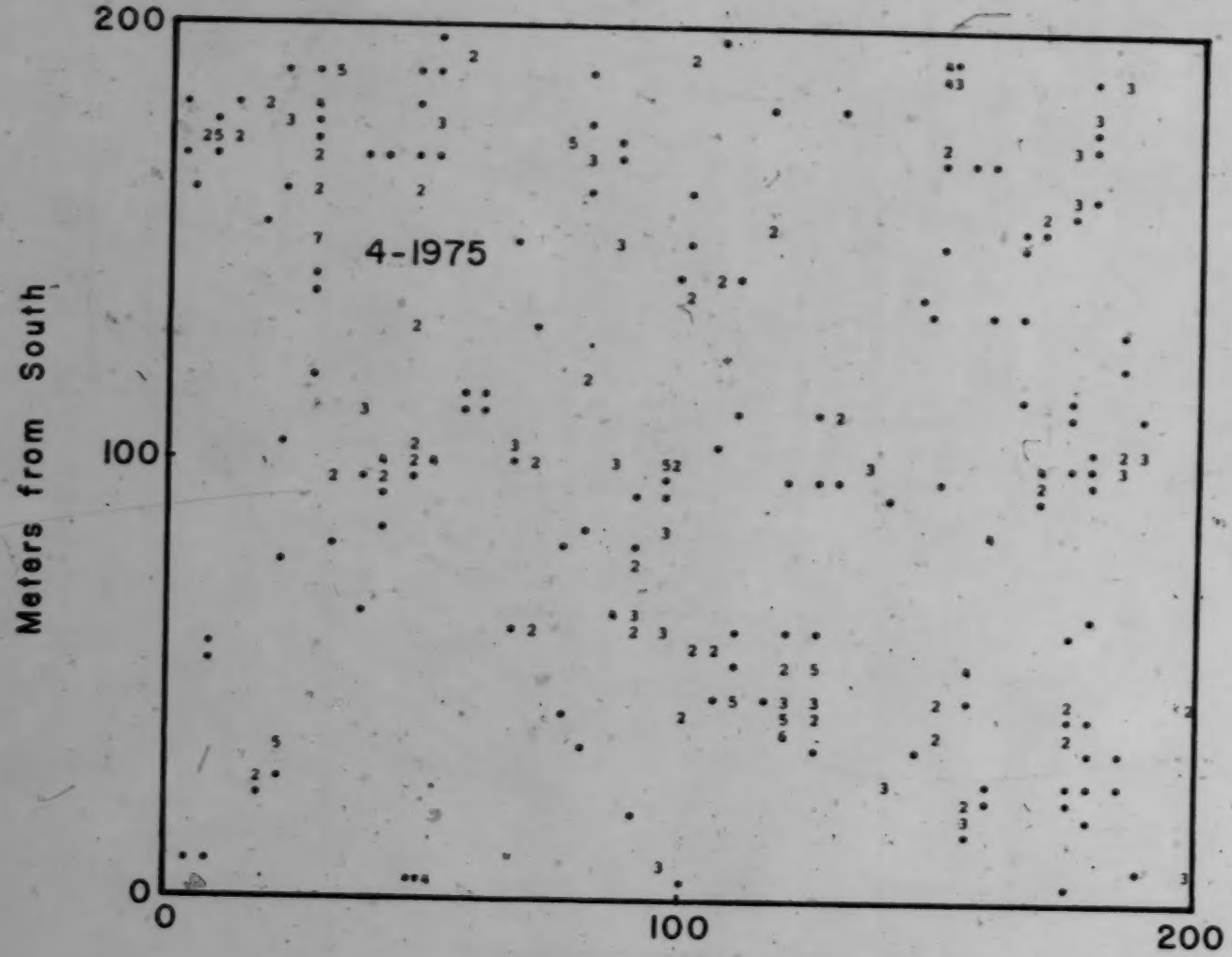
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Meters from South
Meters from West
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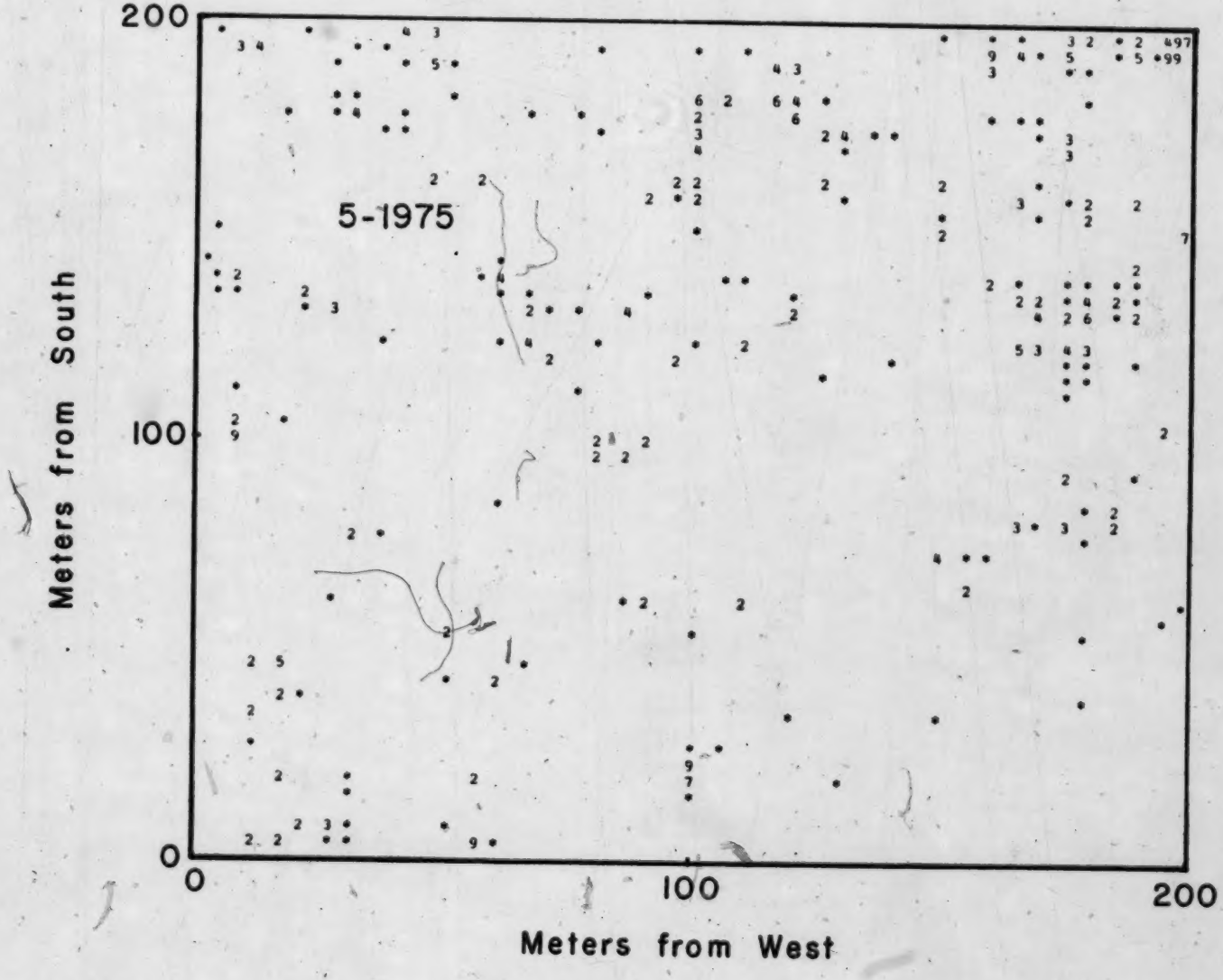
100
200
0
100
200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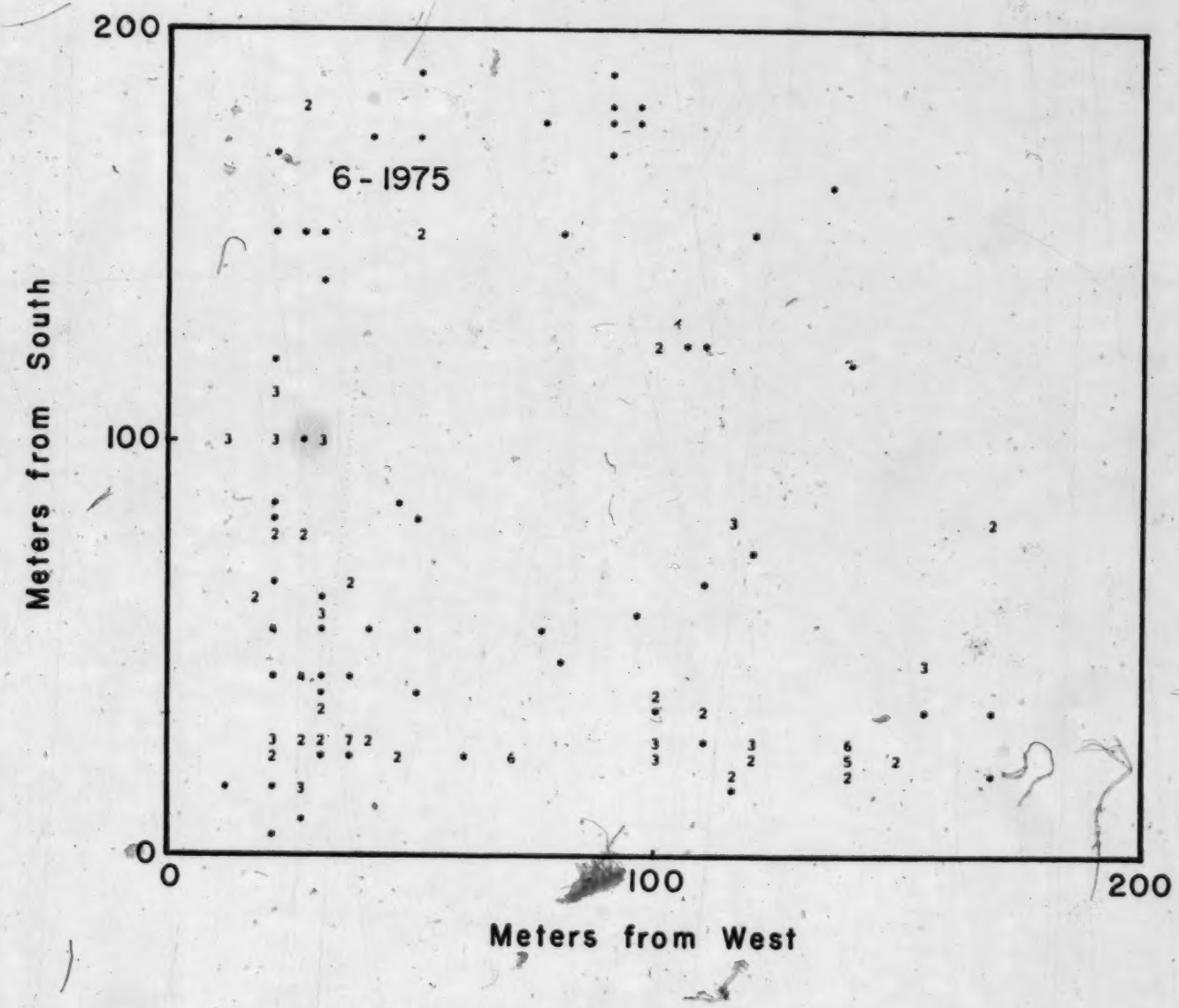
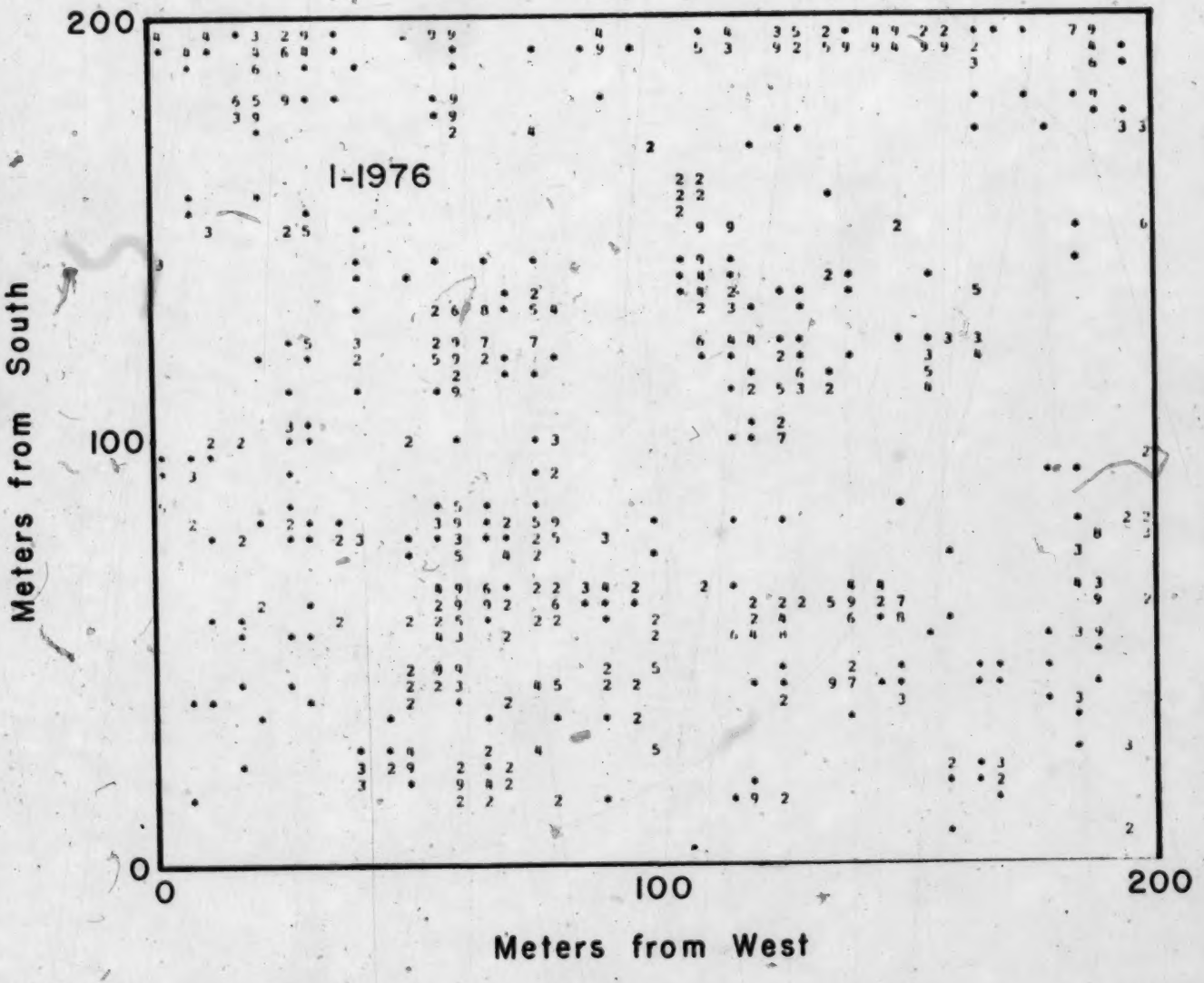
100
0
0
100
200
Meters from South
Meters from West


6-1975
200
100
0
0
100
200
Meters from South
Meters from West


1-1976
200
100
0
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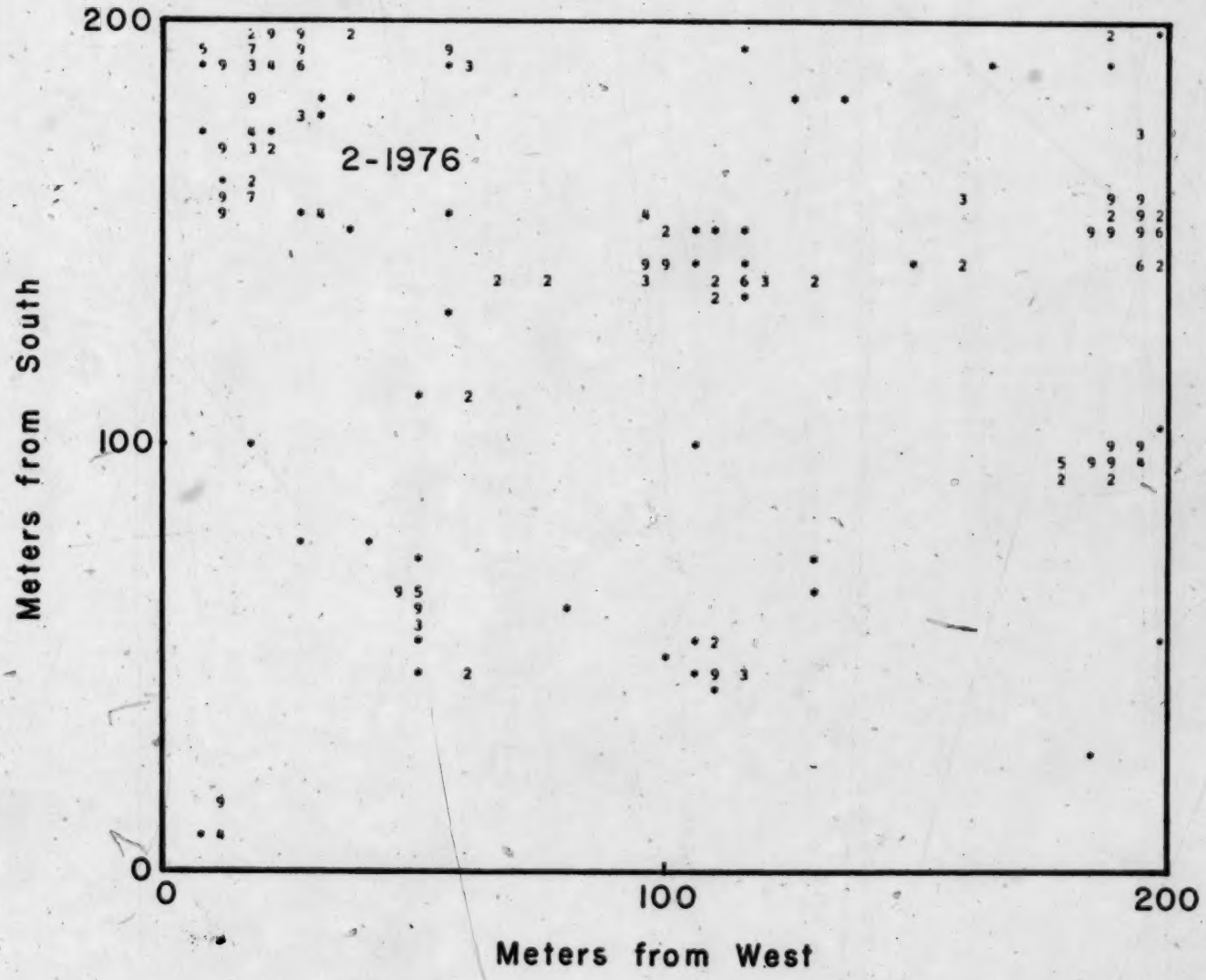
100
200
Meters from South
Meters from West


2-1976
Meters from South
Meters from West
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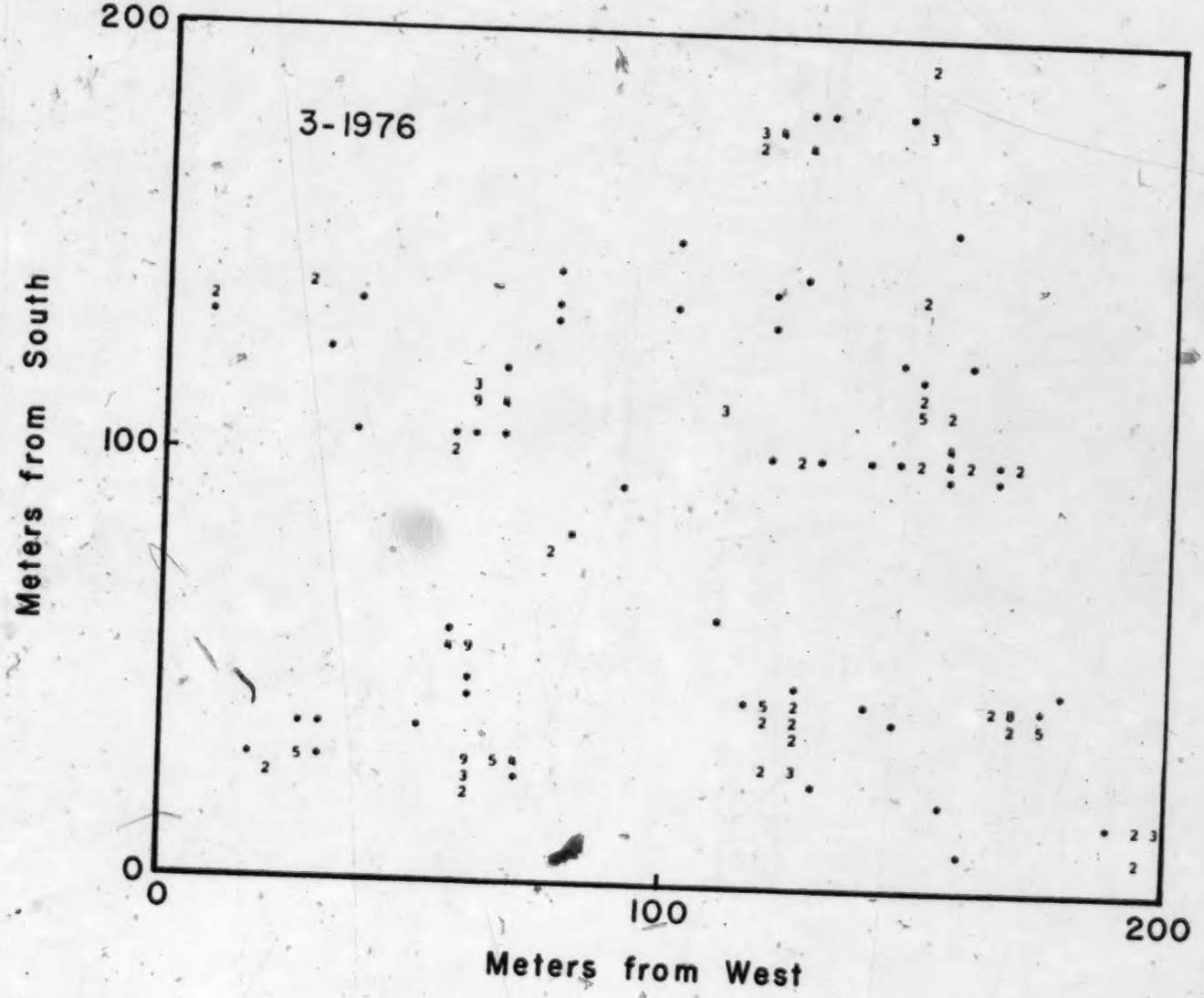
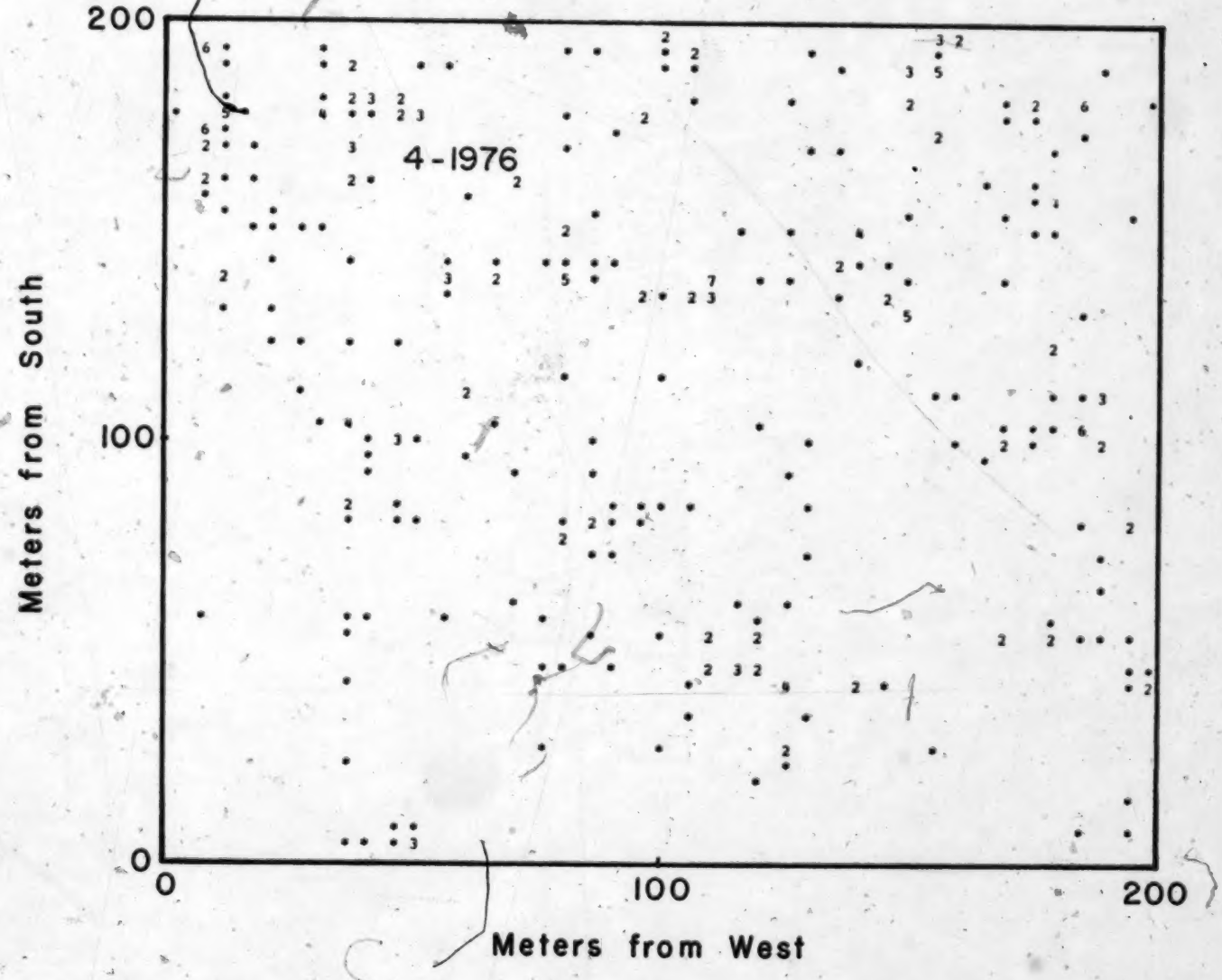
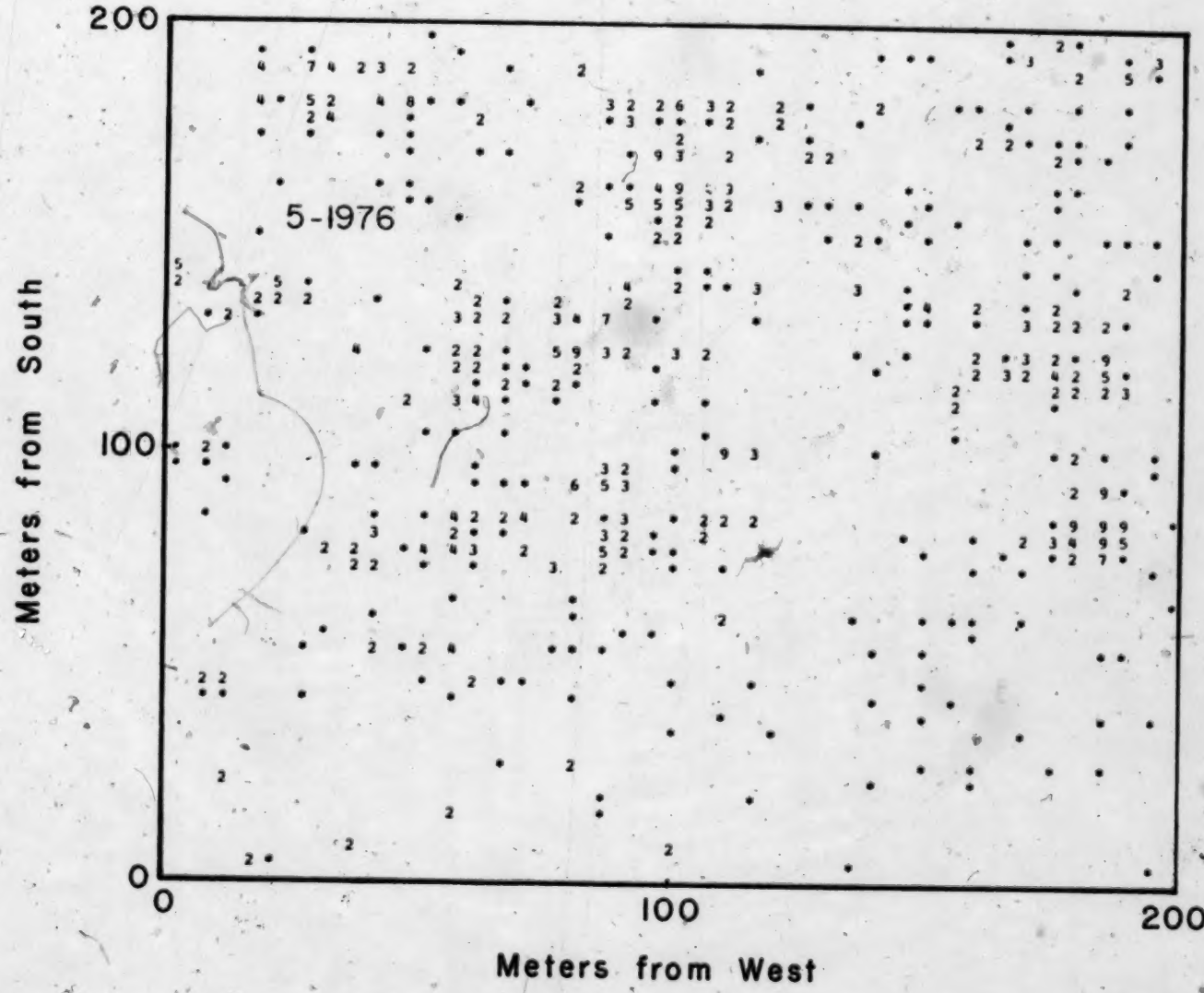
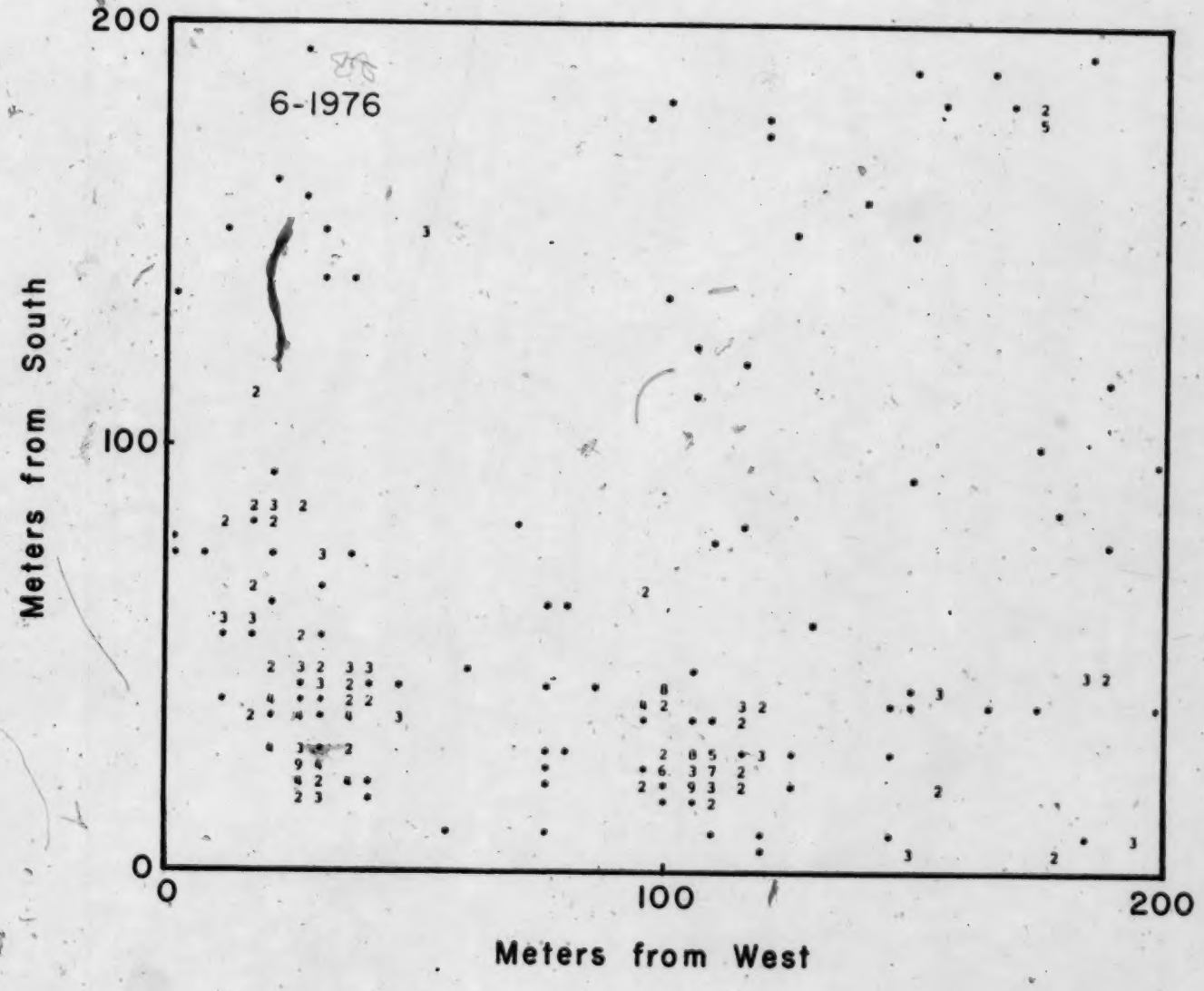

3-1976
200
100
0
0
100
200
Meters from South
Meters from West


4-1976
Meters from South
Meters from West
0
100
200
0
100
200


5-1976
200
100
0
0
100
200
Meters from South
Meters from West


6-1976
200
100
0
0
100
200
Meters from South
Meters from West